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THE QUEENSLAND JOURNAL OF AGRICULTURAL SCIENCE

VOL. 5. NO. 4.

DECEMBER, 1948

PHYLLODY IN THE PAPAW (*Carica papaya*).

By T. McKNIGHT, M.Sc., Pathologist, and S. L. EVERIST, B.Sc., Botanist, Science Branch.

During the course of investigations into the virus causing "yellow crinkle" disease of the papaw (*Carica papaya* L.), interesting examples of phyllody have been observed. Though this condition was mentioned by Simmonds (1938), no detailed observations were given. It is considered that a description of the very marked development of phyllody in plants infected with the virus would be of interest to other workers.

In normal female flowers (Plate 1A) the calyx lobes are about the same length as the tube (i.e., 2–3 mm.), narrowly triangular or deltoid in outline, closely adpressed to the petals, and nerveless. The petals are normally cream coloured and imbricate and at the base remain closely clasped around the fruit until the tips begin to wither. They are lanceolate and thickened at the base. The ovary is cream coloured and ovoid. The stigma is usually about 1 cm. long and is a very pale lemon-yellow.

In a plant infected with yellow crinkle the most conspicuous feature is the green colour of all of the flower parts. There is usually some enlargement of the calyx lobes without any corresponding increase in the size of the calyx tube. In extreme cases the calyx lobes are markedly divergent, leaflike, linear to linear-spathulate and up to 6 cm. long, with a prominent white midrib and conspicuous reticulate veins which are often pink to red in colour. The calyx lobes are sometimes undulate on the margins. The petals are also leaflike, spreading, the basal thickening not so marked as in uninfected plants, narrow-lanceolate to linear, sometimes with conspicuous reticulate veins, often pinkish-red in colour.

The ovaries of infected plants vary considerably. In the majority the ovary is pale green to leaf-green, much smaller than normal, with the stigma reduced to a very small white or pale-cream coloured branched structure less than 0·1 cm. long. Often the ovary develops unevenly and is irregularly ovoid in shape with an eccentric style.

Plate 1.

Normal and yellow-crinkle infected flowers. A. Normal female flower. B. Carpels leaflike but still fused in central flower (petals removed). Right hand lateral flower shows reduced green ovary. C. Carpels leaflike but still fused. D. (All petals and 1 calyx lobe removed.) Phyllody of carpels well developed. Three petioles fused and two fused separately.

In some cases the carpels become foliaceous. The phyllody of the carpels is of particular interest in that many degrees of development of the foliaceous condition may be seen in infected plants. Plates 1 (B, C and D) and 2 (A and B) illustrate some of the variations of this condition. In the extreme condition, the five carpels develop into leaves with a hollow petiole up to 6 cm. long and a peltate lamina not unlike that of a normal foliage leaf except that it is practically undivided. These carpellary leaves apparently all rise in one plane. One flower examined showed four instead of five carpellary leaves, two of them 4 cm. long and two 2·5 cm. long (Plate 2A). Within the whorl of carpellary leaves the receptacle looks exactly like a normal growing point with the young leaves rising in a spiral.

Plate 2.

Yellow-crinkle infected flowers. Left: Flower with 4 carpellary leaves, 2 small and 2 long. Right: Phyllody of carpels very well developed; 4 of the petioles are partly fused, but are easily separable.

Between this extreme condition and that described above for the majority of infected flowers, various degrees of fusion may be present in the petioles of the carpellary leaves. Some are completely connate with only the laminae free; in a few instances they are fused to the tips of the laminae as well, though there is marked difference in texture and venation between the petiole and the laminae. Some specimens have the petioles connate at the very base and the remainder more or less fused, separating easily and without apparent damage to any tissue (Plate 2B).

When phyllody of the carpels is well developed the leaf blades present characters reminiscent of virus symptoms in foliage leaves. For example, the blade may be cupped upwards, sometimes blistered or bullate, the veins slightly raised, and the main vein thickened and raised and with a finely zigzag path.

The condition described is similar to that observed in plants infected with the tomato big-bud virus (Lycopersicum virus 5). Field evidence suggests that the yellow-crinkle virus is identical with this virus and experiments to examine this suggestion are in progress.

The reversion of carpels to leaves is of interest to botanists in that it lends weight to the classical theory of the foliar origin of the carpel.

REFERENCE.

SIMMONDS, J. H. 1938. In Queensland Department of Agriculture and Stock Agricultural and Pastoral Handbook, Vol. III. Brisbane: Government Printer.

THE YELLOW-WINGED LOCUST, *GASTRIMARGUS MUSICUS* FABR., IN CENTRAL QUEENSLAND.

By I. F. B. COMMON, M.A., B.Agr. Sc.*

E.M.N.

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SUMMARY.

Gastrimargus musicus Fabr. is an endemic locust species with a distribution practically throughout coastal and sub-coastal Australia, where the rainfall exceeds 20 inches annually. Swarming occurs in the northern half of the continent and migrations into coastal agricultural and dairying districts occur periodically.

Coastal infestations originate in localized outbreak areas in the sub-coastal districts. In central Queensland, the Clermont-Capella area was apparently the vital source of swarms which eventually caused widespread damage, particularly to pasturage, between 1939 and 1947 from Proserpine to Mt. Larcom.

Biometrical studies show that samples of swarm populations differ in morphology and coloration from samples of isolated individuals. The swarming phase or phase gregaria is characterized by relatively long wings; short, broad and level pronotum; slight sexual dimorphism; and predominantly dull, medium-brown coloration. Phase solitaria has relatively short wings; long, narrow and arched pronotum; marked sexual dimorphism; and predominantly green and dark-brown coloration. Samples of non-swarming individuals with intermediate characters belong to phase transiens.

The five nymphal instars are described. The habits of the nymphs and adults are similar to those of other gregarious locusts. During outbreaks, two generations of phase gregaria occur each year in central Queensland. In the laboratory, the period required for nymphal development in the spring was 50 to 60 days and in the summer and autumn 44 days. Eggs hatch in about 17 days in the summer.

Natural enemies of the eggs, nymphs and adults are recorded, but in the coastal districts at least the control exerted by these appears to be ineffective.

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Various control measures have been tested against nymphal bands of G. musicus. Poisoned baits have been the most efficient, particularly those incorporating the gamma isomer of benzene hexachloride as the toxic ingredient. Molasses appears to be a desirable addition to benzene hexachloride baits to improve palatability.

The ultimate aim of control practice would be the accurate mapping of outbreak areas both in central and in northern Queensland with the object of destroying incipient swarms before mass migrations commence. Once large-scale invasions of the remainder of the infestation area have begun, then complete control seems impracticable. Temporary protection of valuable agricultural crops is possible if a co-operative campaign of poisoned baiting is undertaken.

INTRODUCTION.

Periodically swarms of the yellow-winged locust, *Gastrimargus musicus* Fabr., cause widespread damage to pastures and agricultural crops north of latitude 25 degrees south. During 1939–47 an outbreak of this species occurred in central Queensland, and, as little information was available concerning the life history, habits and phase characteristics of *G. musicus,* it was decided to investigate these matters concurrently with control problems while swarms were active near Rockhampton, where the author was stationed from 1945 to 1948. The tests with various insecticides were undertaken with the full realization that toxicity trials against locusts do not readily yield data capable of statistical analysis.

DISTRIBUTION OF G. MUSICUS.

Distribution of Non-swarming Individuals.

Non-swarming examples of *G. musicus* have been recorded from a large area of coastal and sub-coastal Australia receiving a rainfall of not less than 20 inches per annum, and occasionally specimens occur in districts with a slightly lower rainfall. Most records come from the eastern coastal belt from Melbourne to Mossman, though other records from south of the tropic include Perth and Albany (Western Australia) and Kangaroo and Flinders Islands (Key, 1938).

In the Callide Valley during 1939–47 isolated individuals were more plentiful in native grassland, particularly where tall grass was interspersed with small bare patches of ground. Fields of Rhodes grass (*Chloris gayana*) adjacent to these native pastures were apparently unattractive while the native grasses were available. Lightly timbered or ringbarked country clothed with native grasses was also favoured. On the other hand, the denser stands of timber were avoided.

G. musicus forms part of a varied Acridid fauna commonly occurring in native pastures. The species most frequently observed in this association are *Locusta migratoria* L., *Austracris guttulosa* Walk., *Oedaleus australis* Sauss. and *Acrida turrita* L. Under suitable conditions the first three of these are liable to swarm.

Distribution of Swarms.

The history of outbreaks of *G. musicus* prior to 1937 is particularly scanty (see Weddell, 1937; Key, 1938). This can be understood when it is realized that much of the area in which swarms occur from time to time is sparsely populated pastoral country. The majority of records prior to 1937 refer to swarms affecting the more thickly populated coastal sugar-cane growing districts, but this does not necessarily mean that they have been more numerous in those areas. Outbreaks extending to the coast have enabled more detailed observations to be undertaken on the habits and behaviour of the insect, though it cannot thereby be deduced that its behaviour is always identical in the drier sub-coastal portions of the continent.

Between 1903 and 1908, swarms of *G. musicus* were reported from the Herbert River, Charters Towers and Rockhampton. Again in 1911–2 and 1914–6 there were reports of widespread damage due to this species in central and northern Queensland. It seems possible that these were referred to the one outbreak extending from 1911 to 1916, the actual build-up of swarms occurring in inland areas a year or two before the first reports. Since this phenomenon appears to be confined to the grazing areas between the 20- and 25-inch isohyets and is not necessarily spectacular, it would probably have attracted little attention. In 1911–2 swarms had already reached the coast at Mossman, Cairns and Townsville and were sufficiently numerous to cause concern throughout a large area of the central highlands, particularly at Springsure and Clermont. Apparently this outbreak maintained its intensity to some extent during 1913, especially in the central highlands, though it received no specific mention that year. However, swarms were prevalent during 1914–5 throughout a vast area in central Queensland, Springsure being regarded as the centre of the outbreak. Fliers had migrated to the coast in the Burdekin delta, apparently from the Charters Towers district, and the following year (1915–6) hatchings were reported from egg-beds established near Townsville, on the lower Burdekin and on the Herbert River. No further records of this outbreak are available, so it can be assumed that swarms disappeared.

In February, 1930 loose swarms were reported from Wyndham, in the Kimberley district of Western Australia. There are records of further swarming of *G. musicus* in central and northern Queensland between 1930 and 1935. Swarms reached the coast and damaged sugar-cane in 1930-1 and they were also reported from central Queensland and the Richmond-Hughenden area in 1933–4. No doubt egg-beds were established by the autumn generation of fliers in the latter districts, for hopper bands were present during the following spring. The adults of this generation were reported to have migrated northwards towards the Gulf and Cape York Peninsula (Weddell, 1937).

In the Northern Territory and north-western Australia large swarms were reported in 1935–7 at Brock's Creek, Pine Creek, Hall's Creek and Broome. Egg-beds were established near Broome in 1936, but the adults which reached maturity in this area disappeared. Swarms did not extend farther south than Broome.

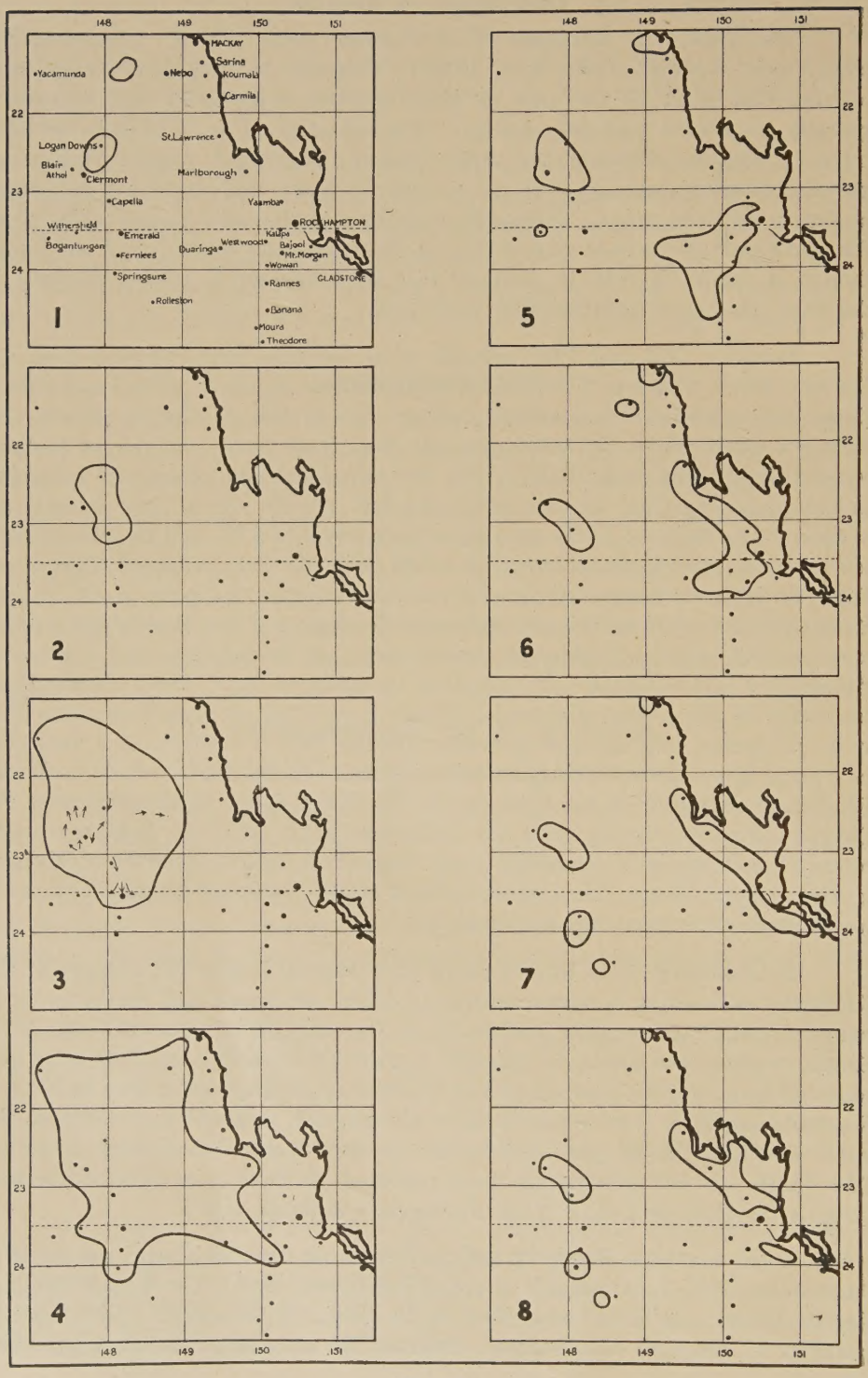

Plate 1.

Maps showing the progress of the 1939-47 outbreak of *G. musicus* in central Queensland.

The 1939-47 Outbreak in Central Queensland.

Records relating to locusts have been made since 1938 by officers of the Locust Information Service, inaugurated by the Commonwealth Council for Scientific and Industrial Research and operated in conjunction with the State Departments of Agriculture. However, except where they refer particularly to central Queensland, no attempt will be made to review fully reports of swarms since 1938.

It has been pointed out (Key, 1938) that coastal infestations of *G. musicus* may be due to invasions of these areas by fliers from the sub-coastal districts of lower rainfall. This hypothesis has been substantiated by observations during the 1939–47 outbreak in central Queensland. Appendix A contains a summary of reports and observations having direct reference to the incidence of swarms of *G. musicus* in central Queensland since 1939.

Available records concerning the origin of the widespread infestation of *G. musicus* in central Queensland between 1939 and 1947 suggest that the most critical area for the build-up of swarms is the Logan Downs-Clermont-Capella sector. However, prior to the first record of swarms in this area, hopper bands and flier swarms were noted on Glenden station, west of Nebo. In March, 1939 *G. musicus* was causing some concern at Glenden and, according to one grazier in this district, there was a gradual build-up of swarms west of Nebo for a couple of years prior to 1939 (Plate 1, fig. 1).

The first flier swarms in the Clermont district were reported in November, 1939 and hopper bands were noted on Logan Downs, about 30 miles north-north-east of Clermont, in February, 1940. No great significance was attached to these swarms until the infested area had increased gradually in dimensions to include the country north-east of Capella by the following year (Plate 1, fig. 2). No great migrations from the area between Logan Downs and Capella were observed until January, 1942, when swarms extended to 40 miles north of Clermont and as far south as Emerald. By the winter of 1942, egg-beds were located over an extensive area, and during the following spring hoppers were hatching from egg-beds from Yacamunda to Capella and also as far east as the Isaacs River. This area had increased slightly by the beginning of 1943 (Plate 1, fig. 3).

The autumn of 1943 saw a considerable extension of the area infested by swarms. The greater migrations of fliers were towards the coast, as far east as Marlborough, though the Springsure district had also been invaded. There was, however, a simultaneous diminution in the incidence of swarms north of Clermont. Towards the end of 1943, fliers had penetrated the Pioneer Valley, west of Mackay, and had extended along the central-western railway to Westwood and thence to the Dawson Valley at Wowan (Plate 1, fig. 4). The year 1943 marked the maximum distribution of swarms, and though other districts, particularly on the coast, were still to be invaded, swarms disappeared subsequently from many of the sub-coastal areas affected during 1943.

During the autumn of 1944, swarms of *G. musicus* continued to advance into coastal areas. These migrations occurred chiefly in the Mackay and Rockhampton hinterlands, though it seems certain that swarms must have persisted in the coastal area between these centres, particularly at St. Lawrence and Marlborough. Swarms invaded the city of Mackay and reached their maximum density in the Pioneer River cane districts in February. Near Rockhampton, swarms extended to within six miles of the city at Gracemere and were also present at The Caves, about 13 miles north of Rockhampton. In the Dawson Valley fliers penetrated to Moura, just north of Theodore; this is the farthest south swams have ever been recorded in this region. Fliers were still active in a restricted area north of Capella and at Withersfield, west of Emerald (Plate 1, fig. 5).

Further local extensions in the incidence of flying swarms occurred during the spring of 1944 and the autumn of 1945. The area north of the Pioneer River was invaded in February, 1945 but the swarms were reported to be numerically weaker. Swarms were also prevalent in the area from St. Lawrence to Rockhampton and at Dululu, in the Dawson Valley. Apart from a restricted area from Capella to Clermont, no reports came from centres west of Westwood. Some hopper activity was observed in the Nebo district, but since then there have been no reports of swarms from this centre (Plate 1, fig. 6).

Minor alterations in the distribution of swarms of *G. musicus* occurred during the latter half of 1945 and in 1946. In most areas swarms were smaller and often numerically weaker. The southern border of the infested area had been extended slightly to include Raglan and swarms were also present at Torilla. By the end of 1946 the pest had disappeared completely from the Dawson Valley and also from all districts immediately west of Rockhampton. Springsure was again affected and some hopper activity was reported from Springwood and Consuelo stations, about 30 miles south-east of Springsure. Swarms persisted in the Capella-Clermont area (Plate 1, figs. 7 and 8).

Only slight extensions of areas previously infested occurred in 1947; these were chiefly in the Yeppoon district and towards Mt. Larcom, south of Raglan. In most other affected districts swarms, though frequently quite dense, were much fewer in number. Swarms had disappeared completely from the Mackay district. At the close of the year, reports were received that the spring-generation bands of hoppers had in many cases died out and that flier swarms which had survived were smaller.

The Course of a Typical Locust Outbreak.

Key (1938) has given an outline of the course of a typical outbreak of the Australian plague locust, *Chortoicetes terminifera* Walk. It is interesting to compare the features of the 1939–47 outbreak of *G. musicus* in central Queensland. Certain favourable conditions of micro-climate and food supply enable a grasshopper population to build up in a circumscribed "outbreak area." Sooner or later, conditions permitting, a critical density of the swarms is reached in the outbreak area and mass migrations of fliers occur. These migrations continue, with the establishment of egg-beds over increasingly greater

areas, until the margins of the "infestation area" are reached. The infestation area is defined as "the area in which swarms of the species have been known to occur." This must be distinguished from the "distribution area" or "the area in which the species lives permanently, irrespective of abundance or phase (if any)." In the case of *C. terminifera,* the outer limits of the infestation area are usually reached and the numbers of locusts are decreasing by the end of the second season of migration. This numerical reduction is noticeable first in the outbreak areas, where it can be ascribed to parasites and predators. By the third season the numbers of locusts in the infestation area have so decreased that only small areas occur where locusts may be still numerous. This reduction can probably be ascribed to adverse climatic conditions. Simultaneously with the decline in other parts of the infestation area there may be an increase in the outbreak areas and, if conditions are again favourable, a second outbreak may occur. On the other hand, adverse conditions at this stage may postpone any further outbreaks for an indefinite period.

The general course of the 1939–47 oubreak of *G. musicus* in central Queensland is somewhat similar. It seems probable that one and perhaps the chief outbreak area of *G. musicus* in this region is the district near Clermont. This outbreak area cannot be defined accurately from the available data, but it almost certainly includes Logan Downs and perhaps also Peak Downs. It is possible that a second outbreak area occurs west of Nebo, but the importance of this area in the 1939–47 outbreak is obscure.

Conditions favourable for an increase in the local population of *G. musicus* in the Clermont area must have occurred in the years 1939–42. What these conditions were is not known accurately, but no doubt rainfall, with its effect upon vegetation and therefore availability of food, was a major factor. The years 1939 to 1942 were good pasture years in the Clermont district, the rainfall being above the average of 26·65 inches.

The major migrations of *G. musicus* occurred in the summer and autumn of 1942 and 1943, with further less extensive migrations in 1944. Apparently the critical population density for the species was reached in the outbreak area by the beginning of 1942. As the migratory flights reached the outer margins of the infestation area in 1944, there appears to have been a considerable weakening of populations in the outbreak area, though swarms continued to persist in this region. With slight exceptions, swarms had penetrated to the outer extremities of the infestation area by the end of 1946, and at this stage dense concentrations were again causing concern in the Capella-Clermont area. Marginal concentrations were represented by swarms in the Mackay hinterland, in the coastal strip from St. Lawrence to Raglan and at Springsure and Springwood. It remains to be seen whether the weakening and disappearance of swarms at the margins of the infestation area will be followed by a complete cessation of swarming activity in the outbreak area. Reports received towards the end of 1947 suggested that, though hoppers hatched in the spring from egg-beds near St. Lawrence, South Yaamba, Yeppoon and Bouldercombe, most

had died out during a rainy period in November. At Ambrose, and in the Clermont district, hoppers reached maturity. In both instances very few egg-beds were subsequently established.

Sundry observations during the course of this outbreak in central Queensland may throw some light on the actual causes of diminutions in the incidence of swarms in the infestation area since 1945. Key (1938) has suggested that adverse climatic conditions are the most important factor in reducing numerically swarms of *Chortoicetes terminifera* infesting the margins of the infestation area. This is in contrast to parasitism, which may at times be a contributing factor in reducing the incidence of swarms in the outbreak area. Though parasites were active from time to time in swarms of *G. musicus* in coastal areas, the control exerted by them appeared to be very limited.

Numerous instances of hopper bands dying out because of food scarcity during dry periods were recorded. Overwintering eggs hatch in the spring when temperatures exceed a certain minimum and sufficient moisture is available. In central Queensland spring rains usually result from scattered thunderstorms, which in some cases have been sufficient to enable eggs of *G. musicus* to hatch yet insufficient to promote growth of grass during the nymphal period. Consequently, hopper bands formed under these conditions perish. On the other hand, reports from the Mackay district, which receives a more reliable and abundant rainfall than the coastal belt near Rockhampton, state that excessive wet weather was probably the major cause of the reduction of hopper bands in that area.

One discrepancy of note exists between the course of this outbreak and the typical outbreak of *C. terminifera* outlined by Key. Whereas outbreaks of the Australian plague locust usually persist for at most three years, the outbreak of *G. musicus* described above persisted for a much longer period. This, of course, may be exceptional for the species, since most of the earlier records suggest that outbreaks have been less prolonged.

The outbreak area in the Clermont district has an average rainfall of approximately 27 inches per annum. The major migrations of swarms to the coastal belt between St. Lawrence and Rockhampton did not commence until the summer and autumn of 1943-4. It is perhaps instructive to note that the years 1944–6 were years of sub-normal rainfall in central Queensland. The rainfall at Rockhampton for these three years was 24·0, 23·8 and 25·8 inches compared with the average for 71 years of 39·0 inches. Actually, therefore, the rainfall in central coastal Queensland from 1944 to 1947 was virtually sub-coastal in type and consequently suitable for the persistence of swarms of *G. musicus*. Thus, the prolongation of the outbreak quite conceivably could have been due to the sub-normal rainfall experienced during the years 1944–6.

Frequently other gregarious Acridid species occur in swarms of *G. musicus*. Specimens of *Chortoicetes terminifera* Walk., *Austracris guttulosa* Walk. and *Oedaleus australis* Sauss. have been collected from time to time. A

Plate 2.

Map of coastal and sub-coastal central Queensland showing isohyets and observed limits of the infestation area of *G. musicus* (dotted line).

single fifth instar nymph of *Locusta migratoria* L. was collected from a nymphal band of *G. musicus* at Barmoya in March, 1947. This specimen approximated well the gregarious coloration of the species described by Uvarov (1928).

THE PHASE THEORY AND BIOMETRICS OF G. MUSICUS.

Phase Theory.

Since the phase theory of locusts was first formulated by Uvarov (1921), he and a number of other workers have confirmed its application to many of the migratory Acridids. The theory, in brief, postulates that the biological, morphological and colour characters of each species are liable to variation within wide limits depending upon the nymphal environment. With a suitable alteration in the environment a transformation from one phase to another may result, though this is a gradual process and may extend over one or more generations. Behaviour differences between the phases are of most significance, but they are associated with certain morphological and colour differences which are capable of more exact analysis.

Three unstable biological states of a locust are recognized by Uvarov and Zolotarevsky (1929). The majority of individuals belonging to a dense, gregarious population exhibit characters typical of *phase gregaria,* while the majority of those living in isolation exhibit characters typical of *phase solitaria.* The term *phase transiens* applies to populations in process of transformation from one extreme phase to the other and the majority of its individuals exhibit intermediate characters.

The alteration in environment necessary for the transformation of one phase into another has been produced artificially by a number of workers. Faure (1932) showed, in the case of *Locusta migratoria* L. and *L. pardalina* Walk., that the coloration and the shape and dimensions of certain parts of the body, both relative and absolute, are more or less constant for adults reared from nymphs subjected to the same environmental stimuli. Furthermore, the colour and morphological characters approaching those of phase gregaria could be produced in the progeny of typical solitary individuals by crowding the nymphs together in cages—that is, by simulating a gregarious environment.

The practical recognition of the phases is accomplished by studying a representative sample from each locust population. Uvarov (1921), working with *L. migratoria,* showed that the wings of phase gregaria are relatively longer and the pronotum is relatively less convex, shorter and broader than those of phase solitaria. Coloration varies considerably in both gregaria and solitaria, but this variation is much less in the former. Phase solitaria is characterized by a much higher percentage of green and dark-brown to black individuals. Finally, sexual dimorphism is less marked in the case of phase gregaria, the size of the males differing but slightly from that of the females in any one swarm.

Biometrical Data.

Key (1938 and 1939) recognized that individuals of *G. musicus* taken from a swarm varied in colour and shape from those taken from a solitary population. In the course of the investigations reported here, these differences were apparent and biometrical data have been compiled in order to ascertain the extent and significance of the variation. Exact measurements were made of numerous examples collected from solitary populations and swarms. These and other collections were also classified according to their coloration.

Dry, pinned specimens with the wings folded in the natural resting position were used in all cases for measurements. The length of the hind femur and the length and the height of the pronotum were measured directly under a low-powered compound microscope equipped with a movable stage and vernier scale reading to 0·1 mm. Measurements of the width of the head were made with a pair of dividers and the distance between the points measured, correct to 0·1 mm., with the compound microscope. The length of the forewing or elytron was measured with a pair of dividers and the readings estimated to the nearest 0·1 mm. on a millimetre rule.

The following symbols have been used in the tables of biometrical data :—

E—length of elytron, taken from the fork of the veins Sc and R to the extreme tip of the wing, as adopted by Faure (1932).

F—length of hind femur.

P—greatest length of the pronotum.

H—height of the pronotum, from the lower extremity in a vertical line to the middle of the dorsum.

C—width of the head at its widest point.

These measurements were used to calculate the ratios generally adopted in biometrical work on locust populations. Mean measurements of each series of examples were calculated by adding the individual measurements and dividing the sum by the number of examples measured. The ratios E/F, P/C and H/C were derived from the mean measurements. Lean (1936) pointed out that average ratios are sometimes misleading. To avoid this the ratios of each individual example have been calculated and the more reliable frequency tables constructed. The degree of sexual dimorphism is expressed as the percentage that the average length of the female elytron is of the average length of the male elytron.

Material Used for Measurements.

Ten series of specimens taken under various conditions and from various localities in Queensland have been used to compile the biometrical data. Since the ratios obtained for male and female series differ quite markedly, the data for the two sexes are presented separately in Tables 1 and 2.

Series I. is a collection of 43 males and 15 females taken at random from a small but dense swarm at Gracemere in March, 1947. This and the material in series II. were taken by holding a collecting net from the side of a motor car at about 18 inches above the ground while driving through the flying swarm.

Series II. comprises 24 males and 12 females collected from a large dense swarm at Bouldercombe in March, 1947.

Series III. is a small collection of 8 males and 8 females taken at random from a dense swarm establishing an egg-bed near Yeppoon in March, 1947.

Series. IV. comprises 19 males and 20 females from a large swarm which established an egg-bed at South Yaamba in March, 1947. The specimens were dead when collected in June, 1947, but were in a good state of preservation. They had congregated in large numbers in the shelter of logs in the egg-bed site, where they had died. The individuals were collected at random but odd specimens with frayed wing-tips were rejected as unsuitable for measurement.

Series V. is a small group of 3 males and 4 females collected by W. J. S. Sloan in April, 1943 from swarms at Clermont, Blair Athol and Emerald.

Series VI. is a collection of 21 males and 14 females made in Rockhampton during February and March, 1947. Though no swarms had been recorded in the actual locality where the collection was made, swarms were active at the time a few miles away. The individuals, though apparently behaving as a solitary population, were quite common.

Series VII. includes 21 males and 7 females collected in June and July in the same locality as series VI. It seems likely, therefore, that the individuals in series VII. were the progeny of those in series VI. Specimens were much less common in June and July.

Series VIII. is a collection of 32 males and 27 females made at Biloela, in the Callide Valley, in February and March, 1947. Individuals were quite common. Biloela is beyond the known infestation area of *G. musicus*, the nearest swarms having been at Dululu, about 45 miles north of Biloela, in December, 1945.

Series IX. is a solitary male specimen taken at Sandgate in February, 1931 and well beyond the limits of swarms of *G. musicus*.

Series X. is a small collection of 12 males and 1 female made at Gayndah by A. W. S. May in March, 1947. This locality also appears to be well beyond the known infestation area for the species.

In all, 184 males and 108 females were measured in order to compile the data presented. Two further series (Ia. and IIa.), taken from swarms at Gracemere and Bouldercombe in March, 1947, were classified into their respective colour groups and these data have been included in Tables 9 and 10.

Discussion of Biometrical Data.

E/F ratios: The E/F ratio is the one most generally used in the biometrical study of a locust population, though other ratios provide valuable supplementary information. It has been shown that the swarm environment tends to increase the relative length of the wings. The E/F ratio of any given locust population is a measure of the relative length of the wings and is therefore a useful criterion of its biological status.

Table 1.

Biometrical Data, all Collections; Males.

	Series and Locality.	No. of Examples.	Mean E.	Mean E/F.	Mean P/C.	Mean H/C.	Degree of Sexual Dimorphism.
			mm.				
Swarming.	I. Gracemere ..	43	34·3	1·73	1·26	1·17	114·3
	II. Bouldercombe ..	24	34·1	1·73	1·23	1·14	117·0
	III. Yeppoon ..	8	37·1	1·72	1·27	1·18	110·8
	IV. South Yaamba	19	36·1	1·71	1·23	1·09	115·8
	V. Clermont-Emerald	3	34·9	1·71	1·22	1·11	112·6
Non-swarming.	VI. Rockhampton ..	21	31·6	1·77	1·28	1·16	122·1
	VII. Rockhampton	21	31·4	1·70	1·36	1·22	126·4
	VIII. Biloela ..	32	31·8	1·68	1·34	1·22	129·2
	IX. Sandgate ..	1	29·0	1·62	1·38	1·17	..
	X. Gayndah ..	12	29·0	1·61	1·33	1·27	126·9

Table 2.

Biometrical Data, all Collections; Females.

	Series and Locality.	No. of Examples.	Mean E.	Mean E/F.	Mean P/C.	Mean H/C.
			mm.			
Swarming.	I. Gracemere	15	39·2	1·82	1·17	1·13
	II. Bouldercombe	12	39·9	1·82	1·19	1·12
	III. Yeppoon	8	41·1	1·82	1·18	1·12
	IV. South Yambaa	20	41·8	1·79	1·19	1·11
	V. Clermont-Emerald	4	39·3	1·78	1·15	1·11
Non-swarming.	VI. Rockhampton	14	38·6	1·81	1·19	1·11
	VII. Rockhampton	7	39·7	1·76	1·25	1·18
	VIII. Biloela	27	41·1	1·74	1·27	1·20
	X. Gayndah	1	36·8	1·69	1·20	1·19

The frequency distribution of the E/F ratios of the 10 series of *G. musicus* is presented in Tables 3 and 4. The maximum frequency for the series I. to V., taken from swarms, lies between 1·70 and 1·77 for males and between 1·78 and 1·85 for females. The mean E/F ratios for these series varies from 1·71 to 1·73 for males and 1·78 to 1·82 for females. The maximum frequency of the E/F

ratios in series IX. and X., solitary individuals taken from localities well outside the infestation area, lies between 1·58 and 1·61 for males. The mean E/F ratios are 1·61 and 1·62. The solitary female example in these collections has an E/F ratio of 1·69. It would appear, therefore, that if the ratios of the small collections of solitary specimens are typical of all solitary *G. musicus*, then the difference between phase gregaria and phase solitaria is well defined.

On the other hand, the E/F ratios of series VI. to VIII. do not differ markedly from those of the swarm collections. It will be noticed, however, that the mean E/F ratio of series VIII. is 1·68 for males and 1·74 for females, while the variation is much greater than in series I. to VII. The examples comprising series VI. to VIII. were all non-swarming individuals and may therefore be

Table 3.

Frequency Table, E/F Ratios.

All Collections of *G. musicus*; Males.

Series and Locality.	E/F Ratios.										
	1·46 1·49	1·50 1·53	1·54 1·57	1·58 1·61	1·62 1·65	1·66 1·69	1·70 1·73	1·74 1·77	1·78 1·81	1·82 1·85	1·86 1·89
I. Gracemere	..	..	..	..	2	8	11	14	7	1	..
II. Bouldercombe	..	..	..	1	2	3	6	5	4	2	1
III. Yeppoon	..	..	..	..	1	2	2	2	1	..	..
IV. South Yaamba ..	..	..	..	1	1	2	8	4	2	1	..
V. Clermont-Emerald ..	..	..	..	..	..	1	1	1	..	..	..
VI. Rockhampton .. .. (February-March)	..	..	..	..	..	3	3	3	7	4	1
VII. Rockhampton .. (June-July)	..	..	..	1	2	7	5	2	1	..	1
VIII. Biloela	1	..	2	..	6	5	8	3	1	..	..
IX. Sandgate	..	..	..	..	1	..	..	..	..	..	..
X. Gayndah	..	1	1	5	1	3	..	..	..	..	..

regarded as phase transiens. The Biloela collection appears to be nearer phase solitaria than either of the Rockhampton collections.

It is not surprising that the E/F ratios of the first Rockhampton collection (series VI.) are high, for the specimens were collected within a few miles of active swarms and had probably developed from hopper-band stragglers. The second Rockhampton collection (series VII.) was made three months later in the same locality and could possibly be the progeny of the fliers which were

Table 4.

FREQUENCY TABLE, E/F RATIOS.

All Collections of *G. musicus*; Females.

Series and Locality.	E/F Ratios.									
	1·58 1·61	1·62 1·65	1·66 1·69	1·70 1·73	1·74 1·77	1·78 1·81	1·82 1·85	1·86 1·89	1·90 1·93	1·94 1·97
I. Gracemere	..	..	..	1	2	4	7	1	..	..
II. Bouldercombe ..	..	..	..	1	..	3	5	2	..	1
III. Yeppoon	..	..	..	1	..	3	2	1	1	..
IV. South Yaamba ..	..	..	..	2	6	6	3	1	2	..
V. Clermont-Emerald	..	..	..	..	2	1	1	..	..	..
VI. Rockhampton .. (February-March)	..	..	..	1	1	7	4	1	..	..
VII. Rockhampton .. (June-July)	..	..	..	3	2	2	..	..	..	..
VIII. Biloela	1	4	5	2	6	2	5	1	1	..
X. Gayndah	..	..	1	..	..	..	..	..	..	..

active in February and March. There were no flier swarms in the Rockhampton district when this collection was made. The mean E/F ratio of series VII. is lower than in series VI. and the variation is greater.

From this data it would appear to be quite practicable to separate the phases of *G. musicus* by means of their E/F ratios, though it is believed that other characters should also be taken into consideration. The E/F ratios of phase gregaria are apparently greater than 1·71 for males and 1·78 for females, while those of phase solitaria are less than 1·62 for males and about 1·72 for females. Populations with intermediate E/F ratios may be regarded as phase transiens.

P/C and H/C ratios: The relative dimensions of the pronotum of the gregarious Acridids provide a useful criterion for the differentiation of the phases. The maximum width of the head is used as the standard of comparison. The solitary phase of many species is characterized by a relatively long and narrow pronotum, the dorsum of which, in some cases, appears strongly convex when viewed in profile. A relatively short and broad pronotum is a feature of individuals from a gregarious population. In profile the pronotum is almost level or sometimes slightly concave. The ratio P/C is a measure of the relative length of the pronotum, while the ratio H/C indicates its degree of convexity.

The frequency distribution of the various P/C ratios are presented separately for males and females in Tables 5 and 6. For gregarious males

Table 5.

FREQUENCY TABLE, P/C RATIOS.
All Collections of *G. musicus*; Males.

Series and Locality.	P/C Ratios.										
	1·08 1·11	1·12 1·15	1·16 1·19	1·20 1·23	1·24 1·27	1·28 1·31	1·32 1·35	1·36 1·39	1·40 1·43	1·44 1·47	1·48 1·51
I. Gracemere	..	1	5	10	12	3	8	2	1	1	..
II. Bouldercombe	4	1	4	4	4	4	2	1	..	..	..
III. Yeppoon	..	1	..	..	4	2	..	..	1	..	..
IV. South Yaamba ..	..	1	2	4	9	2	1	..	..	..	..
V. Clermont-Emerald ..	..	..	1	1	..	1	..	..	..	..	..
VI. Rockhampton .. .. (February-March)	..	..	5	..	5	2	5	2	1	..	1
VII. Rockhampton .. (June-July)	..	..	..	..	2	2	8	5	2	2	..
VIII. Biloela	..	..	..	1	4	5	10	4	3	2	..
IX. Sandgate	..	..	..	..	..	..	..	1	..	..	..
X. Gayndah	..	..	..	1	2	2	2	4	1	..	..

Table 6.

FREQUENCY TABLE, P/C RATIOS.
All Collections of *G. musicus*; Females.

Series and Locality.	P/C Ratios.								
	1·08 1·11	1·12 1·15	1·16 1·19	1·20 1·23	1·24 1·27	1·28 1·31	1·32 1·35	1·36 1·39	1·40 1·43
I. Gracemere	1	4	6	3	1	..	..	..	..
II. Bouldercombe	1	3	3	4	..	..	1	..	..
III. Yeppoon	..	4	2	1	..	1	..	..	..
IV. South Yaamba	4	1	4	7	2	1	..	..	..
V. Clermont-Emerald ..	..	1	1	..	..	..	..	..	..
VI. Rockhampton .. .. (February-March)	1	3	3	5	2	..	..	..	..
VII. Rockhampton .. .. (June-July)	..	..	1	2	1	3	..	..	..
VIII. Biloela	..	..	4	4	6	8	1	1	2
X. Gayndah	..	..	..	1	..	..	..	..	..

Table 7.

FREQUENCY TABLE, H/C RATIOS.
All Collections of *G. musicus*; Males.

Series and Locality.	H/C Ratios.									
	1·00 1·03	1·04 1·07	1·08 1·11	1·12 1·15	1·16 1·19	1·20 1·23	1·24 1·27	1·28 1·31	1·32 1·35	1·36 1·39
I. Gracemere	..	1	6	11	13	5	5	2	..	..
II. Bouldercombe ..	..	5	3	6	5	2	3	..	..	..
III. Yeppoon	..	..	2	2	1	1	..	2	..	..
IV. South Yaamba ..	1	7	6	3	1	1	..	..	..	..
V. Clermont-Emerald	..	..	2	..	1	..	..	..	..	..
VI. Rockhampton .. (February-March)	..	1	1	7	6	4	1	1	..	..
VII. Rockhampton .. (June-July) ..	..	1	..	..	5	6	6	2	1	..
VIII. Biloela	..	1	1	3	6	8	8	4	1	..
IX. Sandgate ..	..	..	..	..	1	..	..	..	..	..
X. Gayndah	..	..	..	..	1	..	5	5	..	1

(series I.–V.) the maximum frequency lies between 1·24 and 1·27 and for females between 1·16 and 1·19. The maximum frequency for solitary males (series IX. and X.) lies between 1·32 and 1·39 while the P/C ratio of the solitary female from these collections is 1·20. The differences between the P/C ratios for phase gregaria and phase solitaria therefore appear to be clearly defined.

As would be expected if the values given for the E/F ratios are an authentic index, the P/C ratios for phase transiens (series VI.–VIII.) are intermediate between those of phase gregaria and phase solitaria. The maximum frequency for series VII. and VIII. indicates that these populations more nearly approximate phase solitaria than does the population represented by series VI.

The frequency distribution of H/C ratios for series I. to X. is presented separately for males and females in Tables 7 and 8. The maximum frequency for the males in series I. to V. lies between 1·12 and 1·15 and for females between 1·08 and 1·15. The average H/C ratios for males vary from 1·09 to 1·18 and for females from 1·11 to 1·13. The maximum frequency for the males in series IX. and X. lies between 1·24 and 1·31, while the average ratios vary from 1·17 to 1·27. The H/C ratio of the solitary female from Gayndah is 1·19. Again the ratios for the Rockhampton and Biloela collections (series VI.–VIII.) are intermediate between those of phase gregaria and phase solitaria.

Table 8.

Frequency Table, H/C Ratios.

All Collections of *G. musicus*; Females.

Series and Locality.	H/C Ratios.									
	0·96 0·99	1·00 1·03	1·04 1·07	1·08 1·11	1·12 1·15	1·16 1·19	1·20 1·23	1·24 1·27	1·28 1·31	1·32 1·35
I. Gracemere	..	..	3	..	7	5	..	..	..	..
II. Bouldercombe ..	1	..	3	2	4	1	..	1	..	..
III. Yeppoon	..	1	..	4	2	..	..	1	..	..
IV. South Yaamba ..	1	2	2	6	4	2	1	1	..	..
V. Clermont-Emerald	..	..	..	1	1	..	..	..	..	..
VI. Rockhampton .. (February-March)	..	....	2	6	4	..	1	1	..	..
VII. Rockhampton .. (June-July)	..	..	..	..	3	1	2	1	..	..
VIII. Biloela	..	..	..	1	4	9	6	5	1	1
X. Gayndah	..	..	..	..	..	1	..	..	..	..

Sexual dimorphism: The length of the elytron of locusts has been accepted generally as a reliable criterion of the absolute size of the specimens (Johnston and Maxwell-Darling, 1931; Faure, 1932; Lean, 1936). Measurements of the total length of the insects from the frons to the tip of the wing are not a satisfactory index, for the head of pinned specimens is sometimes stretched forward or retracted slightly beneath the pronotum.

The mean elytron length for the 10 series of *G. musicus* is included in Tables 1 and 2. Whereas the mean length for the various female collections varies from 36·8 to 41·8 mm., there appears to be no consistent difference between those for females taken from swarms and those for non-swarming females. The data do not, however, give a true indication of the mean length of the elytra of females from phase-solitaria populations, since only one example was available for measurement. The male collection data, on the other hand, show that males from swarms are larger than males from solitary populations. The mean elytron length of the swarm collections (series I.–V.) varies from 34·1 to 37·1 mm., compared with a mean length of 29·0 mm. for phase solitaria. Phase transiens has mean elytron lengths of 31·4 to 31·8 mm., values intermediate between those of phase gregaria and phase solitaria.

The degree of sexual dimorphism has been calculated for each series; it varies from 112·6 to 117·0 for phase gregaria and from 122·1 to 129·2 for phase transiens. The value 126·9 given for series X., phase solitaria, is based on one female example only and is therefore not reliable (Tables 1 and 2).

The marked difference between the absolute sizes of males and females from solitary populations is a feature of most Acridid species. It has been stated (Lean, 1936) that the decrease in the degree of sexual dimorphism associated with the transformation of phase solitaria to phase gregaria probably has an important biological value. Unless the males of a flying swarm approximate the size and, therefore, presumably the flight capacity of the females, the sexes would soon become segregated during migration when considerable distances are covered each day.

Colour Variation.

G. musicus, like other gregarious Acridids, shows a marked colour variation and this can generally be correlated with phase variation. Green individuals are found more commonly amongst solitary examples, though odd green specimens are often observed in swarms. This colour variation is characteristic of the nymphs as well as the adults.

The typically gregarious coloration of adult males is a uniform dull medium-brown with few darker markings. The dark oblique stripes of the head are inconspicuous and are seldom well defined on the pronotum. Gregarious females are usually medium- to dark-brown with well defined oblique stripes on the head, extending to the pronotum in most instances. Males with a dark-brown pronotum and conspicuous facial markings, as well as green individuals of both sexes, also occur in swarms. The intensity of the green coloration in these variants is far from constant.

It was found practicable, when classifying the material according to coloration, to differentiate three male and two female colour groups. Males were classified into green, dark-brown and typically gregarious coloration (light- to medium-brown); females were divided into two groups, green and dark-brown. The percentage of individuals in the series I. to X. belonging to each colour group is set out in Tables 9 and 10.

Table 9.

Classification into Colour Groups.

All Collections of *G. musicus*; Males.

Series and Locality.	Phase.	No. of Examples.	Percentage Green.	Percentage Dark-brown.	Percentage Typically Gregarious Coloration.
I. Gracemere	gregaria ..	43	9·4	11·6	79·0
Ia. Gracemere	gregaria ..	74	6·8	5·4	87·8
II. Bouldercombe ..	gregaria ..	24	8·3	8·3	83·3
IIa. Bouldercombe ..	gregaria ..	127	..	..	100·0
III. Yeppoon	gregaria ..	8	..	12·5	87·5
IV. South Yaamba ..	gregaria ..	19	..	..	100·0
V. Clermont-Emerald ..	gregaria ..	3	..	..	100·0
VI. Rockhampton ..	transiens ..	21	14·3	38·1	47·6
VII. Rockhampton ..	transiens ..	21	..	100·0	..
VIII. Biloela	transiens ..	29	27·6	27·6	44·8
IX. Sandgate	solitaria ..	1	..	100·0	..
X. Gayndah	solitaria ..	12	41·7	41·7	16·7

Green examples were found to occur more commonly amongst females. In males the dark-brown coloration apparently is as typical a solitary character as green. It must be pointed out, however, that the dark-brown colour group of females includes a variety of colour shades from grey, through dark-brown, to nearly black. No consistent colour character could be discerned to subdivide this group, though this may be practicable when larger collections of phase-solitaria females are examined.

Table 10.

Classification into Colour Groups.

All Collections of *G. musicus*; Females.

Series and Locality.	Phase.	No. of Examples.	Percentage Green.	Percentage Dark-brown.
I. Gracemere	gregaria ..	15	6·7	93·3
Ia. Gracemere	gregaria ..	16	12·5	87·5
II. Bouldercombe	gregaria ..	12	16·7	83·3
IIa. Bouldercombe	gregaria ..	40	12·5	87·5
III. Yeppoon	gregaria ..	8	12·5	87·5
IV. South Yaamba	gregaria ..	20	5·0	95·0
V. Clermont-Emerald	gregaria ..	4	..	100·0
VI. Rockhampton	transiens ..	14	42·9	57·1
VII. Rockhampton	transiens ..	7	14·3	85·7
VIII. Biloela	transiens ..	27	55·6	44·4
X. Gayndah	solitaria ..	1	..	100·0

The normal nymphal coloration of phase gregaria was never maintained under laboratory conditions when nymphs were reared from the egg or first instar. When dense populations were maintained, either in glass jars or in a breeding cage, 21 by 18 by 24 inches, with glass top and front and gauze sides and back, nymphs without exception became almost black after the first moult.

Nymphs which were isolated in glass tubes from the time of hatching showed a wide variation in colour. First instar nymphs were of normal coloration, but the subsequent instars varied from green, grey, reddish-brown, dark-brown to almost black. The majority of the second instar nymphs were various shades of light- to medium-grey with indistinct markings, though one was rich brown in colour and another green. Of 30 third instar nymphs, 3 had assumed a green coloration, 19 light grey, 4 light brown, 1 medium brown, 2 very dark brown and 1 slightly paler than the normal gregarious coloration. The markings of all but the last specimen were much less distinct than normal. Of 22 fourth instar nymphs, 4 were green, 1 greenish-grey, 9 light grey, 4 light brown, 1 medium brown, 1 reddish brown and 2 light normal. Of 15 fifth instar nymphs, 4 were green, 2 light grey, 4 light brown, 2 brown and 3 paler than normal. Under the isolated conditions of high humidity, each colour type appeared to be highly unstable. The colour of any one nymph might change two or three times before it reached maturity.

Conclusions Drawn from Biometrical and Colour Data.

Definite conclusions on phase relationships must wait until larger collections of solitary individuals from beyond the infestation area of the species can be examined. There appears, however, to be quite a marked morphological and colour difference between phase gregaria and phase solitaria in *G. musicus*. Phase transiens has characters intermediate between the two. The following summary will serve as a guide to the characters of the phases:—

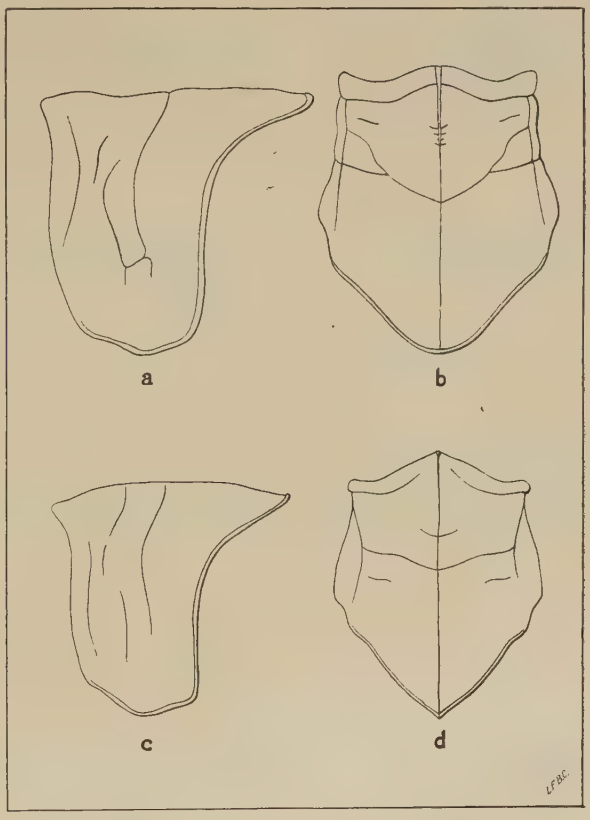

Plate 3.

Dorsal and lateral views of pronotum of male of *G. musicus*. a and b, *Phase gregaria*; c and d, *Phase solitaria*. (Camera lucida drawings.)

Phase Solitaria:

(*a*) Colour very variable; green and dark-brown forms predominating amongst males, green amongst females; facial markings in dark-brown male forms distinct.

(*b*) Pronotum relatively long with the dorsum convex, fore and hind margins angular (Plate 3, figs. c. and d.).

(*c*) Low E/F ratio, probably below 1·62 for males and about 1·72 for females.

Plate 4.

Adults of *G. musicus* ($\frac{2}{3}$ natural size). Top pair: *Phase solitaria,* males; smallest and largest specimens collected. Second row: *Phase transiens,* females; smallest and largest specimens collected. Third row: *Phase gregaria,* males; smallest and largest specimens collected. Fourth row: *Phase gregaria,* females; smallest and largest specimens collected. Bottom pair: *Phase gregaria,* male and female; dorsal view.

(*d*) Strong sexual dimorphism; males much smaller than females (Plate 4).

Phase Gregaria:

(*a*) Colour slightly variable; medium-brown forms with indistinct facial markings predominating amongst males; dark-brown amongst females.

(*b*) Pronotum relatively short with dorsum nearly level or slightly concave, fore and hind margins rounded (Plate 3, figs. a. and b.).

(*c*) High E/F ratio, above 1·71 for males and 1·78 for females.

(*d*) Slight sexual dimorphism; males slightly smaller than females (Plate 4).

It should be emphasized that these criteria must be applied to representative samples of locust populations and cannot be used as a satisfactory guide to the phase status of single specimens. Again, any one criterion should not be used to determine the phase status of a locust population without due consideration being given to the remainder. This is important, for the data show that phase transiens may have one character closely approximating phase gregaria while the other characters are more typical of phase solitaria. Colour and sexual dimorphism appear to be characters most rapidly altered in a changed environment. Thus in series VI.—a population apparently beginning to revert to the solitary phase—52·4 per cent. of the individuals have a typically solitary coloration and the degree of sexual dimorphism is intermediate between phase gregaria and phase solitaria. The E/F ratio, on the other hand, is still typical of phase gregaria.

DESCRIPTION OF STAGES.

Egg (Plates 5 and 6).

Elongate cylindrical, slightly curved with bluntly rounded ends; surface of chorion bears a fine, hexagonal pattern of raised brown protuberances. Freshly laid eggs are light yellow in colour, changing to brown on exposure to the air; eggs in an advanced stage of embryonic development are dull greyish-brown. Dimensions: At oviposition—mean length 5·6 mm. (range 4·7–5·9 mm..), mean diameter 1·4 mm. (range 1·3–1·5 mm.) At hatching—mean length 7·3 mm. (range 7·1–7·6 mm.), mean diameter 1·8 mm. (range 1·6–1·8 mm.).

Vermiform Larva (Plate 5).

Contained in transparent vermiform membrane which ensheaths each appendage separately; head directed downwards beneath the pronotum; antennae directed backwards beneath the pronotum; hind legs usually outstretched; legs non-functional. Colour, pale pinkish-brown with indistinct darker markings.

First Instar Nymph (Plate 5).

Antennae, 12–13 segments, light grey, becoming darker distally.

Head, light grey with small irregular darker markings; a broad, dark band extending obliquely from base of antenna, across lower two-thirds of eye to the posterior margin of head; a narrower, whitish band, parallel and adjacent to the first, from beneath the basal

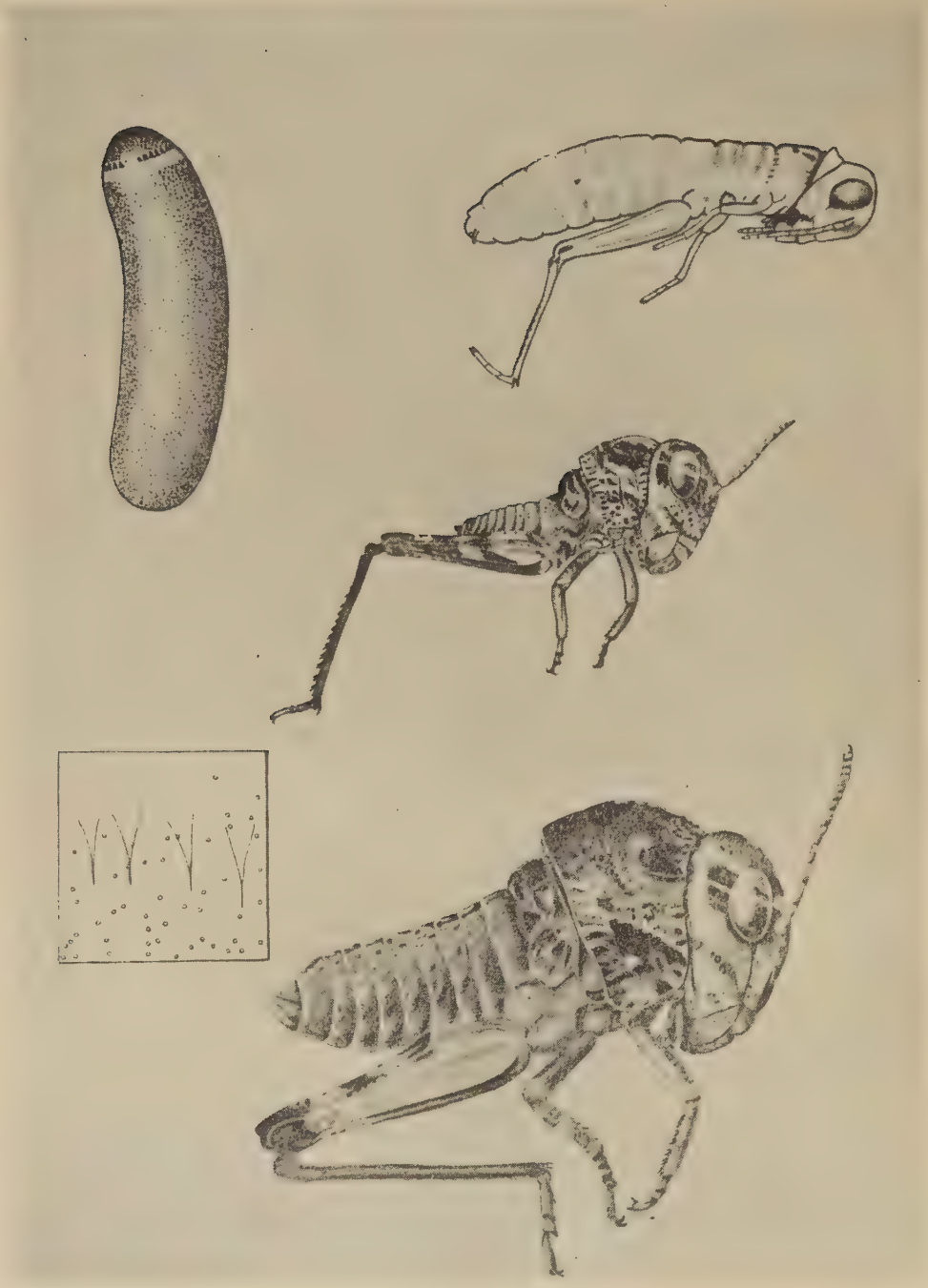

Plate 5.

Life-history stages of *G. musicus*. Egg, vermiform larva and first two instars (x 7·5). Inset: Portion of chorion showing four micropylar canals (x 160). (Camera lucida drawings.)

segment of the antenna, below eye to posterior margin of head; two more narrow bands, parallel to these, extending obliquely across gena, the first dark grey and the second light grey with darker irregular markings. Lower angle of gena, dark grey.

Pronotum, arched; grey with darker irregular markings; the parallel oblique bands of the head continue across the pronotum, the broadest including two raised, dome-shaped, shining black spots near the median keel.

Meso- and meta-thorax and abdomen, grey with darker irregular markings; rudimentary wings visible as dark grey lobes.

Pro- and meso-thoracic legs, grey with darker markings.

Meta-thoracic legs, femur light grey with dark grey to black oblique fasciae; tibia and tarsus dark grey to black.

Dimensions: Newly moulted nymph, mean length 6·0 mm. (range 5·6–6·5 mm.); fully fed nymph, mean length 7·8 mm. (range 7·2–8·5 mm.); length of hind femur, mean 3·5 mm. (range 3·5–3·7 mm.); length of antenna, mean 2·3 mm. (range 2·1–2·4 mm.).

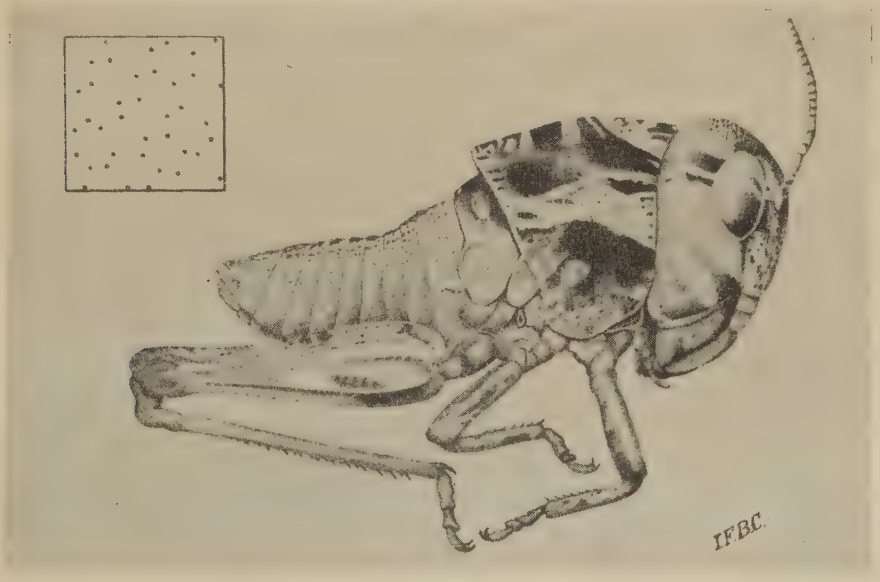

Plate 6.
Third instar of *G. musicus* (x 7·5). Inset: Portion of chorion showing typically hexagonal patterns of chorionic protuberances (x 160).

Second Instar Nymph (Plate 5).

Antennae, 14–16 segments; grey, becoming darker distally.

Head, greyish-brown with small irregular darker markings; a broad, dark greyish-brown band extending from beneath and between the antennae, divided into two narrower parallel bands across the eye to the posterior margin of the head; two narrower dark-brown bands extending back from clypeus and mandible respectively, parallel to the broad dark band.

Pronotum, greyish-brown with small darker greyish-brown, irregular markings; the dark bands of the head extend obliquely across the pronotum as a broken and irregular pattern.

Meso- and meta-thorax, dark brown-black with odd markings; wing-buds showing evidence of venation.

Abdomen, pro- and meso-thoracic legs, greyish-brown with small darker markings.

Plate 7.

Fourth and fifth instars of *G. musicus* (x 4). (Camera lucida drawings.)

Meta-thoracic legs, femur greyish-brown with oblique darker fasciae; tibia and tarsus, dark brown-black.

Dimensions: Newly moulted nymph, mean length 8·2 mm. (range 7·4–9·2 mm.); fully fed nymph, mean length 11·4 mm. (range 9·8–12·8 mm.); length of hind femur, mean 4·9 mm. (range 4·6–5·2 mm.); length of antenna, mean 3·0 mm. (range 2·8–3·2 mm.).

Third Instar Nymph (Plate 6).

Antennae, 17–20 segments.

Description similar to that of the second instar nymph, but markings usually more clearly defined. Wing-buds more developed and showing a rudimentary venation.

Dimensions: Newly moulted nymph, mean length 11·6 mm. (range 10·0–12·5 mm.); fully fed nymph, mean length 15·8 mm. (range 13·6–17·4 mm.); length of hind femur, mean 7·0 mm. (range 5·8–7·5 mm.); length of antenna 4·4 mm. (range 3·6–5·2 mm.).

Fourth Instar Nymph (Plate 7).

Antennae 21–22 segments.

Markings as in the second and third instars but more distinct and darker in colour; ground colour tinged with dull orange-brown, particularly on the head; tip of mandibles bright red.

The wings are drastically changed in this instar. Instead of both wing-buds remaining side by side in a drooped attitude, they have moved up on to the dorsum and the hind pair are placed outside the fore pair. They are much larger than before and the venation is quite distinct.

Dimensions: Newly moulted nymph, mean length 15·3 mm. (range 14·4–16·5 mm.); fully fed nymph, mean length 21·7 mm. (range 20·3–23·0 mm.); length of hind femur, mean 10·0 mm. (range 8·7–10·7 mm.); length of antenna, mean 5·8 mm. (range 5·4–6·2 mm.).

Fifth Instar Nymph (Plate 7).

Antennae, 24–25 segments.

Description similar to the fourth instar nymph; ground colour of head dull orange-brown becoming brighter posteriorly; tip of mandibles bright red; ground colour of pronotum light grey with markings dark brown to black.

Wings much larger and venation of hindwing well developed and pale in colour against the almost black wing membrane.

Dimensions: Newly moulted nymph, mean length 23·0 mm. (range 20·5–25·0 mm.); fully fed nymph, mean length 29·5 mm. (range 26·4–33·6 mm.); length of hind femur, mean 15·5 mm. (range 14·4–16·8 mm.); length of antenna, mean 8·6 mm. (range 8·1–9·4 mm.).

DEVELOPMENT AND HABITS.

Observations have not been made on the life history of the solitary phase of *G. musicus*. The life history of the gregarious phase was studied in some detail at Rockhampton, both in the field and in the laboratory.

Life History.

Egg-beds.

As is the case with other gregarious grasshoppers and locusts, the eggs of *G. musicus* are laid in egg-pods in the soil. The egg-pods are located in relatively well defined areas known as egg-beds, the density of the egg-pods usually varying considerably within any one egg-bed.

The soil and vegetation type as well as the topography of egg-bed sites appear to vary within wide limits. Egg-beds have been recorded on light sandy loams, loams, medium clay-loams and heavy black clay-loams; they have occurred on flats, gentle slopes, ridges, rocky hillsides and even on the tops of hills.

The concentration of the egg-pods in any one egg-bed appears to be influenced by local variations in ground cover and the hardness and moisture content of the soil at the time of oviposition. Once a flying swarm has settled down to oviposit, the females appear to seek out those sections of the site which are relatively bare, with a firm soil surface and a suitable moisture content. In some cases, this limited selection may result in the most concentrated egg-laying occurring in the higher and better-drained parts, while the lower, comparatively water-logged portions are avoided. On the other hand, egg-beds have been observed in which the densest concentrations of egg-pods were in slight depressions which had been filled with water during the previous rains. These depressions apparently fulfilled the moisture requirements when oviposition occurred, the intervening higher ground being too dry and accordingly avoided. Following rain on well-drained soil, otherwise suitable for oviposition, little or no selection appears to be exercised and the concentration of egg-pods may be approximately constant throughout most of the egg-bed.

The vegetative covering in egg-bed areas is also a variable factor. In some cases, open grassland is utilized as an egg-bed site, surplus grass being normally denuded by the fliers before oviposition actually commences. Areas that are already denuded of grass, such as occur on stock routes and in over-grazed pastures, especially where stock congregate near gateways and watering places, are favoured egg-bed sites. In the poorer types of grazing country, particularly on clay-pans where poplar-leafed box (*Eucalyptus populifolia*) thrives, patches of coarse grass are sometimes interspersed with relatively bare ground. Such bare spaces frequently form suitable egg-bed sites, the shape of the egg-bed being governed by the extent and the shape of these spaces. Sometimes egg-beds are established in the inter-row spaces and on the bare headlands of fields of standing crops such as sugar-cane and pineapples.

An excellent example of the localized selectivity exercised by ovipositing females was afforded by an egg-bed established at the forested margin of grassland north of Rockhampton. Oviposition proceeded during the heat of a January day, but apparently because of the high solar temperature the females were massed in whatever shade was cast by trees, fence-posts, bushes and stumps. There was a clear line of demarcation between the dense concentrations of females ovipositing in the shade and the almost completely bare ground without.

Egg-pods deposited in unusual sites were discovered from time to time. At Springsure, an egg-bed extended from a black-soil slope up the rocky side of a ridge to its summit some 150 feet above the surrounding country. In every available patch of soil amongst the rocks, egg-pods were located. Large areas of heavily overgrazed black soil, similar to that at the base of the ridge, could have been utilized for oviposition in preference to the apparently less suitable rocky terrain. Again, near Rockhampton, egg-pods were unearthed amongst the stones on an unused macadamized road.

The densest concentration of egg-pods observed was in an egg-bed located on a heavy black clay-loam at Alton Downs, near Rockhampton, where there were approximately 270 egg-pods per square foot (Plates 8 and 9).

Egg-pods.

Length and shape of the egg-pods of *G. musicus* show considerable variation. The length of 10 egg-pods taken at random from an egg-bed in a clay-loam soil near Rockhampton varied from 2·0 to 3·2 inches, with a mean of 2·7 inches. Following these observations, another egg-pod 3·6 inches in length was unearthed.

The shape of the egg-pods varies from almost straight to strongly bowed. Frequently the latter shape results when the ovipositor of a female strikes a small stone or other hard obstruction beneath the soil surface. The majority of egg-pods are slightly curved, the exit hole reaching the surface almost vertically. The cross-section of the egg-pod is circular and approximately 5 mm. in diameter.

The number of eggs per egg-pod also shows a fairly wide variation. In 10 egg-pods taken at random the number varied from 22 to 57 with a mean of 39. Mungomery (1944) gave the average as 58, while Girault's figure, quoted by Uvarov (1928), was 53.

There is no well-defined wall to the egg-pod. The female, in making the tunnel preparatory to oviposition, smooths and firms the walls and for this purpose a firm, moist soil appears to be ideal. The eggs are laid within the tunnel so formed usually in four but sometimes in three vertical rows with the micropylar end and ventral concave side of each egg directed downwards. This orientation of the egg in the egg-pod is predetermined by its normal position in the ovary, where the micropylar pole of the egg is always posterior and the concave side ventral. The young larva which completes its embryonic development with the head directed away from the micropylar pole is in the most suitable position for its subsequent emergence from the egg-pod.

Plate 8.
Vertical section of egg-pods of *G. musicus* in clod of black clay-loam. (The coin is 1 inch in diameter.)

Plate 9.
Transverse section of egg-pods of *G. musicus* in clod of black clay-loam.

The eggs occupy the lower one-third to one-half of the egg-pod and are glued together with the frothy secretion of the female's accessory glands. The upper portion of the egg-pod is also filled with this material, which is readily penetrated by the emerging vermiform larvae. This secretion is deposited as a white, frothy liquid, but on exposure to the air gradually hardens and changes to a light brown colour. There is no cap to the egg-pod and usually all external signs of the tunnel are obliterated by the thin layer of loosened surface soil generally associated with the activities of numerous ovipositing females.

The Egg and Embryonic Development.

The chorion of the egg bears a characteristic pattern of small brown protuberances. This chorionic sculpturing is absent from certain localized areas, notably where the egg has been in close apposition with its neighbour and also in a narrow circular band about 0·1 mm. in width extending round the egg near the posterior pole (Plate 6). In this latter region the micropylar apparatus is located. It consists of a ring of 46 to 48 funnel-shaped canals which are readily detected *in situ* under the low power of the compound microscope when the egg is immersed in 70% alcohol. The wider part of each funnel opens on the outside of the exochorion and the inner, very fine aperture is directed towards the posterior pole of the egg (Plate 5). In an egg 6·4 mm. in length, the outer funnel-shaped openings were located 0·6 mm. and the inner apertures 0·5 mm. from the posterior pole. Each canal therefore passes through the chorion obliquely (Roonwal, 1936). The micropylar canals allow the entry of the spermatozoa during the actual process of oviposition.

The majority of the chorionic protuberances are arranged in a typical hexagonal pattern, one protuberance at each corner of the hexagon. Between the ring of micropylar canals and the posterior pole of the egg the chorionic sculpturing becomes much denser, a number of protuberances forming each side of a hexagon in the pattern. The density increases in this region as the pole is approached until the protuberances become so concentrated that the pattern is obscured. The colour of the chorion becomes darker accordingly.

Development in the egg is similar in all Acridids. A few days after oviposition a thick serosal cuticle is formed beneath the vitelline membrane, which disappears simultaneously. The serosal cuticle is secreted in two layers; the first is an outer thin yellow cuticle; this is followed by an inner thick laminated white cuticle which is responsible for the toughness of the egg (Wigglesworth, 1939). As the egg develops, the white cuticular layer of the serosa, which is at first thicker than the chorion, gradually becomes thinner until at hatching only the thin yellow cuticular layer remains. At this stage the chorion has usually cracked and peeled off the egg.

Samples of eggs from a number of different egg-beds were dissected in the laboratory during June to ascertain the actual stage of development of the embryo during dormancy. To accomplish this the anterior pole of the egg was removed under water with a sharp scalpel and the contents evacuated by gently

squeezing the remainder of the egg, commencing at the posterior pole. The embryo was then cleared of extraneous yolk particles by directing a fine jet of water at it from a syringe. This technique was recommended by Plotnikov and cited by Uvarov (1928).

Egg samples dissected were all laid by fliers of the summer and autumn generation. Some had been stored in air-dry soil in the laboratory for 15 months and appeared to be still viable. Others were stored either in air-dry soil or on moist cotton-wool in Petri dishes for two and three months. A few had remained in the egg-bed for three months and were collected just prior to dissection. Two samples of eggs which were stored on moist cotton-wool were subjected to a temperature of 2–5°C. for periods of two and four weeks during March and April.

The embryo in all cases was fully differentiated, the eyes and appendages of the head and thorax being readily discerned. Blastokinesis, however, had not commenced. The head was in the vicinity of the posterior pole (that is, the micropylar end) and the embryo measured slightly more than one-third the length of the egg (length of embryo 2·4 mm., length of egg 6·4 mm.). It was white in colour and opaque, with a faint reddish-brown mark visible on the eye from the dorsal aspect. This stage in embryonic development appears to be similar to that observed in other species of grasshoppers during the winter diapause—for example, *Melanoplus differentialis* (Wigglesworth, 1939).

Apparently the pre-blastokinesis stage in *G. musicus* is reached in autumn while the soil in the egg-bed remains sufficiently moist following the summer monsoonal rains. Whether the dormant state in which the egg then remains is an obligate diapause or whether it is necessitated by partial desiccation is not clear. In the field further development normally ceases until the spring, when temperatures become sufficiently high to enable it to proceed. Nevertheless, such development will not continue without moisture, though the viability of eggs which have been stored for a considerable period in dry soil is not affected. In the laboratory, eggs of the summer generation which had been stored in air-dry soil from April, 1946 until February, 1947 hatched 14 days after they were placed on moist cotton-wool in a Petri dish.

During development the eggs increase considerably in size. Samples of eggs were measured by means of a vernier scale on the movable stage of a compound microscope. The mean length of 10 eggs, measured within two hours of oviposition, was 5·6 mm. (range 4·7 to 5·9 mm.) and their mean diameter 1·4 mm. (range 1·3 to 1·5 mm.). Eggs overwintering in the laboratory lose their turgidity and the yolk becomes viscous in consistency. The mean length of 10 such eggs was 5·9 mm. (range 5·7 to 6·1 mm.) and the mean diameter 1·3 mm. (range 1·1 to 1·5 mm.). On the other hand, 10 eggs which were about to hatch had a mean length of 7·3 mm. (range 7·1 to 7·6 mm.) and a mean diameter of 1·76 mm. (range 1·6 to 1·8 mm.). Thus eggs had increased in length from 5·6 mm. at oviposition to 7·3 mm. at hatching and in diameter from 1·4 mm. at oviposition to 1·76 mm. at hatching.

A corresponding increase in the weight of the egg occurs during embryonic development. Twenty eggs which were collected in the field in May, 1946 and stored in air-dry soil in the laboratory until October, 1946 weighed 0·1403 gm. After being exposed to moisture for a further five days on cotton-wool in a Petri dish their weight had increased to 0·3378 gm., 2·4 times their original weight.

In the field, soil type appeared to influence the actual date of hatching. The lighter soil types required less rain than did the heavier soil types to provide suitable conditions for later embryonic development. This is believed to be determined by the availability of free moisture in the soil, for plant growth also responds to light rains much more readily on light soils than on heavy soils. Consequently, eggs in egg-beds separated only by short distances, but on different soil types, may hatch at different times.

Sometimes egg-beds are established during relatively dry periods on low-lying ground subject to temporary flooding during the monsoonal rains. It is therefore a question of very practical importance how long eggs can remain immersed without losing their viability. In considering this question it is desirable to know what stage of development the embryo has reached when immersion takes place. Laboratory tests were carried out to throw some light on this problem.

Twenty eggs taken from an egg-pod in which hatching had commenced were immersed in one inch of water for four days. They were then incubated at room temperature on moist cotton-wool. Hatching was delayed six to eight days, including the period of immersion. All of the eggs hatched but only six became normal first instar nymphs. Of the remainder, six died as vermiform larvae, five died immediately following the intermediate moult and three became first instar nymphs deformed in either antennae or legs.

Eighteen eggs of the summer generation which were held in air-dry soil in the laboratory from May, 1946 to February, 1947 were immersed in one inch of water for seven days. They were then incubated at room temperature on moist cotton-wool. Sixteen of these hatched quite normally 20 to 23 days after the commencement of the immersion period. One failed to hatch and another died as a vermiform larva. When immersed the embryos of these eggs had reached the pre-blastokinesis stage characteristic of diapause.

It would appear, therefore, that eggs of *G. musicus* can withstand immersion in water for periods of up to at least seven days. If immersion continues for a period of four days or more when the eggs are ready to hatch, then serious upsets in the normal hatching are likely to occur. In cases where hatching has been delayed by immersion, but is otherwise normal, the delay is due possibly to the lowered temperature rather than to any direct effects of immersion.

Hatching.

Hatching of the eggs of *G. musicus* usually takes place during the morning or the early afternoon. The chorion cracks in a number of places as the time of hatching approaches and frequently peels off quite readily. The writhing movements of the enclosed embryo, together with the periodical swelling of the cervical ampulla, finally fracture the serosal cuticle and a few more energetic movements completely liberate the vermiform larva.

Intermediate Moult.

All of the eggs in any one egg-pod hatch more or less simultaneously, liberating the vermiform larvae, which are enclosed in a transparent skin. This membrane, though covering each appendage separately, allows only writhing movements of the abdomen. In this way the larvae wriggle one after another upwards to the surface through the spongy material used to fill the upper portion of the egg-pod. Shedding of the vermiform larval skin usually begins immediately the surface is reached, though in some cases the vermiform larva spends a moment on the surface before this membrane is fractured.

The actual rupture of the vermiform larval skin is preceded by an energetic writhing of the abdomen and inflation of the cervical ampulla while the larva reclines on its side or back. The rupture follows in the region of the cervical ampulla and the skin rapidly shrinks over the head and thorax and backwards over the abdomen, the pro- and meso-thoracic legs being withdrawn simultaneously. It then quickly shrinks to the end of the abdomen and down the hind femora and tibiae. With the skin still adhering to the tip of the abdomen, the larva withdraws its hind legs completely. Immediately afterwards the young nymph turns over on to its feet with the vermiform skin still adhering to the tip of the abdomen as a small, shrivelled pellet. The shrivelled skin is shed completely in a few seconds and the young nymph begins to hop away.

Large numbers of the small white vermiform skins litter the ground where the larvae have emerged. This is usually the only external sign of the exit, for frequently the surface of the ground at hatching time is covered by a layer of loose soil particles anything up to half-an-inch or more in depth.

In one egg-bed kept under observation, where the egg-pods were densely concentrated in shallow depressions, rain during the winter had filled the depressions with water. The water finally disappeared but in doing so deposited on the surface of the soil a layer of fine silt which had caked hard. At the time of hatching, the hot sun had caused the layer of silt to crack into irregular pieces the edges of which had curled upwards. The young larvae found their way to the original soil surface and thence out through the cracks.

Habits.

Nymphs.

The first instar nymph of *G. musicus* following the intermediate moult is pale pinkish-brown with a few brownish markings, but the normal dark pattern appears during about the first 90 minutes. This normal pigmentation is attained even when the nymph is kept in complete darkness.

Feeding is not commenced until the morning following the intermediate moult and this appears to be the case irrespective of whether hatching takes place in the morning or in the afternoon.

Since egg-beds are usually located on ground with only a sparse vegetative covering, the first instar nymphs begin hopping round in search of food. In the summer, food is usually abundant adjacent to the egg-bed or even on part of it. In early spring, however, there is at first frequently only a very young grass shoot, produced by the rain which enabled the eggs to complete their development. Under both sets of conditions large numbers of nymphs hatching over a period of a few days congregate on the available grass in or on the margin of the egg-bed. This congregating for food appears to be the initial step in the aggregation of hopper bands. Small groups, in moving about during feeding, merge and finally one or more bands are formed which exhibit the usual characteristics of gregarious hoppers.

Though this may be regarded as the normal procedure following the hatching of eggs in egg-beds, it does not follow that gregarious bands will be formed invariably. In some cases, where nymphs have been emerging from an egg-bed in very large numbers, no aggregation of hopper bands has taken place, even though conditions for aggregation appeared to be quite normal.

The younger nymphal instars and frequently the older ones too remain congregated in dense masses, moving about apparently in no definite direction. Feeding usually is most marked during the morning, the time of day when feeding commences being influenced chiefly by temperature. The hoppers of the spring generation thus commence to feed later in the morning than those of the summer-autumn generation. If a dark cloud obscures the sun, feeding is usually greatly reduced and hoppers tend to climb up grass stems and other objects, though there is a certain amount of feeding even on days when the sky is completely overcast. Under cloudy conditions, however, they are more sluggish and bands tend to avoid mass movement over any great distance. As the temperature increases towards the diurnal maximum, typical mass movement is more readily stimulated.

During the wanderings of these nymphal bands, there is a typical massing of individuals at the front margin, while the concentration of hoppers gradually diminishes towards the rear of the band. Here often only a few stragglers may be seen.

As the afternoon advances and the temperature falls, hopper activity gradually slackens until finally, towards nightfall, mass movement ceases altogether. Individual hoppers then climb up any objects which happen to be near. Grass stems, stones, sticks, weeds, stumps and heaps of cow manure soon become smothered with the young hoppers.

It has been observed (Weddell, 1934) that the spring generation hoppers of *Chortoicetes terminifera* in southern Queensland tend to avoid shade. In central Queensland, however, the maximum solar temperatures, when both the spring and summer generations of *G. musicus* hoppers are active, are so high that hoppers always tend to seek shade during the hottest part of the day.

Plate 10.
Third instar nymphs of *G. musicus* massing in shade on a roadway during an October day.

Feeding by the hoppers becomes reduced in intensity about 24 hours before each moult. It ceases altogether some hours before and does not recommence until some hours afterwards. Moulting takes place on a grass stem or other convenient object, with the hopper suspended by the hind tarsi head downwards.

Migrating Swarms.

Sometimes for a day or two after the final moult the first fliers do not take to the wing unless disturbed, but hop about and feed with the remaining fifth instar nymphs. At first they undertake short circling flights which do not extend far beyond the limits of the hopper band. As the number of fliers increases, the flights become more frequent and of longer duration, this activity apparently being stimulated by the flight of other individuals in the swarm. By the time the last nymphs are moulting, flight is much more general and soon the circling flight becomes more sustained and directional.

Migrations may be undertaken by dense or loose swarms. Swarms have been reported, particularly in the Central Highlands, several miles in extent. However, seldom if ever do migratory swarms reach the dimensions of the recorded migrations of overseas species.

Key (1942), in analysing data concerning the outbreaks of *Chortoicetes terminifera,* concluded that swarms tend to fly towards regions of higher humidity. This may also apply to migrating swarms of *G. musicus,* for outbreak areas in this species in central Queensland are located towards the western margin of the infestation area. Major migrations during the 1939–47 outbreak did not occur in a westerly direction.

It should be noted that, though some migration by swarms of *G. musicus* occurred in the spring of 1942 and 1943, the major migration took place in the autumn. This is significant, for it dispels any belief that the major migratory flights of this locust are undertaken in search of food. Uvarov (1928) stated that mass migrations of *Locusta migratoria* are not due to lack of food in its breeding grounds and, furthermore, that emigrating swarms are practically unable to take food in substantial quantity because the digestive organs at this period are largely compressed by the fat body and the air-sacs. In central Queensland, most of the rainfall is received in January, February and March and during these months pastures are particularly lush. Frequently migrating swarms of *G. musicus* leave areas of good pasturage when commencing their major migrations.

Settling of Swarms.

Migrations are not undertaken because of lack of food in the breeding-places, nor are they undertaken in search of suitable oviposition sites. Uvarov (1928) stated that the migratory stimulus is purely physiological in nature and is associated with the maturation of the genital products. With the approach of sexual maturity in the individuals comprising the migrating swarm, the fat body apparently becomes exhausted and the air-sacs reduced in capacity. This necessitates the termination of the migration and further flights are relatively short and circling in character. Locust migrations therefore cannot have a fixed objective, so that the nature of the soil and vegetation in the area occupied by a settled swarm need not necessarily be suitable for feeding and oviposition. The wide variation in the soil type, vegetation and topography exhibited by egg-beds of *G. musicus* appears to provide evidence for concluding that Uvarov's statement applies also to this species.

The behaviour of a swarm which had completed its migratory flight at Bouldercombe was observed during February, 1947. The swarm was first inspected at 9.30 a.m. on February 19 when it occupied an area roughly circular in outline and about 750 yards in diameter. Near the eastern margin of this area the soil was a sandy loam and the ground sloped gently towards a series of shallow waterholes in the western margin. The locusts were feeding on the tall grass which was particularly abundant and succulent in the vicinity of the waterholes. Sections of the swarm made short flights, close to the ground and in a clockwise direction when viewed from the centre of the swarm. A series of clicking sounds is characteristic of the leisurely flight of this species. Only occasional pairs were mating and oviposition had not commenced. It was apparent, however, that an egg-bed was to be established on the higher ground occupied by the swarm.

By Februry 22, oviposition was well under way, though dissections of females taken in flight showed that a considerable percentage had still not reached sexual maturity. Oviposition was almost completed when the egg-bed was again visited on February 26. The odd females remaining in the egg-bed area were either mating or egg-laying. The actual period of oviposition in the case of this swarm was thus about seven days.

Swarms which are preparing to establish egg-beds behave quite characteristically. During the day the individuals of the swarm indulge in the typically short circling flights as they move to their feeding grounds. As nightfall approaches, there is a general drifting of fliers back to the camping site, which almost invariably becomes the egg-bed site. In the late afternoon, this area becomes progressively massed with fliers which reach the site by short leisurely flights. Those already settled do not appear to be readily stimulated to further flight, but usually crawl about on the ground until they have orientated their bodies at right angles to the last of the sun's rays (Plate 11).

Plate 11.

A swarm of *G. musicus* adults camped for the night. Notice the late afternoon sunlight reflected from the elytra of the locusts settled at right angles to the sun's rays.

A vigorous stridulation is maintained by the males while this nightly congregating is in progress. By the time the sun has set, all available grass stems, logs, and even the ground in the camping site are covered by the swarm. All activity and sound cease by dusk. This one restricted camping site is occupied by the swarm each night until egg-laying is completed.

The dispersal of the camped swarm in the early morning is a similarly gradual process, activity apparently being stimulated by an increase in temperature above a certain minimum.

On February 22, early morning observations were made on the progressive activity of the Bouldercombe swarm. It was daylight at about 5.15 a.m. When the observations commenced at 5.55 a.m. there was a perceptible, concerted stridulation. The air temperature was then 69° F. and that at the soil surface

71° F. When disturbed, only short flights of a yard or two were undertaken by the fliers. The stridulatory sound and the general activity gradually increased in volume until 6.40 a.m., when the air and soil temperatures respectively had reached 72° F. and 73° F. Short flights of several yards had commenced by this time and the characteristic clicking sound produced by both sexes in flight was in evidence. None, however, had attempted to leave the camping site. At 7.05 a.m. activity suddenly increased and fairly strong flights to the periphery of the camping site had begun. The majority of those remaining on the ground again orientated themselves at right angles to the

Plate 12.

A crop of maize after three days' attack by a flying swarm of *G. musicus*. Before the invasion commenced the maize was tasselling.

sun's rays. Oviposition and mating had commenced. The temperature of the air and soil surface were both then 77° F. Fliers began their sustained flights to the feeding grounds shortly afterwards when the temperature remained at 77° F.

Food-plants of G. musicus.

Adults appear to favour the native pasture grasses as food, though introduced grasses and crop plants are frequently attacked. Flying swarms will rapidly defoliate such crops as maize (Plate 12), Sudan grass and sorghum and at times have caused considerable foliage damage to sugar-cane. As is the case with hopper bands, couch grass (*Cynodon dactylon*) and paspalum (*P. dilatatum*) are particularly favoured pasture grasses, but Rhodes grass is attacked in the absence of the more palatable species.

Few species outside the Gramineae are included among the food plants of *G. musicus*. Occasionally pineapples (family Bromeliaceae) have been injured, but almost invariably the plants have recovered (Plate 13). It is likely that the fliers attacking pineapples were seeking moisture rather than food. A crop of cotton (family Malvaceae) at Barmoya was said to be largely defoliated by a flying swarm.

Plate 13.

Superficial damage caused by adults of *G. musicus* to young pineapple plants.

Mating and Oviposition.

Mating occurs on the actual egg-bed site. Before the females have reached sexual maturity, the males frequently but unsuccessfully attempt to mate. When the female genital products are mature, little preliminary attention by the male is necessary before mating proceeds. Often a number of males are observed attempting to mate with the one female.

Oviposition commences shortly after mating is completed. The unattended female walks slowly over the ground testing the soil every few moments with the extremity of her abdomen curved beneath her body. When the consistency of the soil appears to be suitable she braces herself and, by a series of pulsating movements of the abdomen and a rhythmical opening and closing of the valves, works her abdomen down into the soil. As the abdomen penetrates the soil it increases gradually in length by the expansion of the intersegmental membranes between segments iii. to vii. Normally the tunnel so formed curves backwards away from the body of the female and not beneath the body as sometimes figured in textbooks.

While the female is ovipositing, she is frequently attended by at least one male which remains astride until the egg-pod is completed. Apparently mating is then resumed (Plate 14).

Ovipositing females and their attendant males are not so easily disturbed as they are before oviposition commences. Of the two, the males are more readily disturbed under these circumstances, while the female appears to have difficulty in removing her abdomen from the oviposition tunnel. Usually flight is attempted by the disturbed females before the abdomen is removed, with the result that the base of the abdomen becomes twisted and finally severed.

Plate 14.

G. musicus adults ovipositing at the edge of a new egg-bed. Notice the males astride the females during oviposition.

The surface of the egg-bed following the activities of the ovipositing females often becomes more or less disturbed, depending on the condition of the soil at the time of oviposition. In some soils the crust which is formed when the surface layer is dried out is broken up into small irregular fragments (Plate 15). In others, where the surface is still comparatively moist, surface disturbance is negligible and the innumerable holes produced by the females testing the suitability of the soil are a feature.

SEASONAL HISTORY.

Detailed life-history studies were carried out in the laboratory with both spring and autumn generations. Individual nymphs were reared in corked glass tubes with a small square of blotting paper lining the cork to control excess condensation. Small tubes, 4 inches in length and 1 inch in diameter, were

found to be quite satisfactory for the first three instars, while larger tubes, 6 inches in length and 1¼ inches in diameter, were suitable for the fourth and fifth instars.

The spring-generation nymphs were fed exclusively on leaves of *Paspalum dilatatum,* but this material tended to raise the humidity in the tubes excessively with some resultant condensation on the glass sides. Nymphs of the first two instars did not appear to be adversely affected by the highly humid conditions, but mortality was heavy in the later instars, with the result that only one

Plate 15.

The surface of an egg-bed of *G. musicus* established on a self-mulching soil. Notice the small irregular fragments of the soil crust disturbed by the ovipositing females.

individual reached maturity. The free moisture in the tubes probably caused the food to become unduly contaminated by the excreta, even though the tubes were thoroughly cleaned and fresh food was provided each morning.

The autumn generation of nymphs was fed throughout with couch grass (*Cynodon dactylon*). This proved to be more satisfactory than paspalum, for not only is couch grass one of the most favoured foods of *G. musicus* but the problem of condensation was overcome. Mortality was accordingly much lower.

As the actual larval duration of individual nymphs reared under solitary conditions might be different from that of nymphs reared under gregarious conditions, batches of nymphs were concentrated in glass jars, 4¼ inches in diameter and 8 inches in height, in the bottom of which was a layer of fine dry sand about 2 inches in depth. In these jars they were reared quite successfully. The concentration of nymphs in the jars was not constant and was reduced considerably as they neared maturity. As many as 150 first instar nymphs were kept in such a jar, but only about 15 fifth instar nymphs.

Material for these breeding jars was hatched from eggs held in the laboratory and also collected from nymphal bands in the field. Nymphs do not assume their normal coloration for some hours after each ecdysis and newly moulted individuals in a band can thus be readily detected. A number of these newly moulted nymphs of the third and fifth instars was collected to supplement the stocks of nymphs reared from eggs in the laboratory. It was assumed that should the artificial conditions of laboratory rearing affect the duration of the various stadia, this would be at least partially offset by introducing fresh material developed under field conditions up to the third and fifth instars. Thus nymphs which had been bred in the laboratory from eggs were discarded when they had reached the third instar, in case the duration of the later stadia was affected by the artificial environment of the earlier instars. Similarly, third instar nymphs collected in the field were discarded when they had reached the fifth instar. For the purpose of compiling the data presented, therefore, no more than two successive stadia were passed by each individual under laboratory conditions.

The average period required for the various stadia is set out in Table 11. It should be noted that the mean nymphal duration of the spring generation reared in glass jars at moderate humidity was 60·2 days compared with a mean duration of 50·2 days for nymphs reared in individual tubes at very high humidity. Both groups were reared in October and November. The mean nymphal duration of the autumn generation reared in individual tubes at high humidity during March and April was 44·1 days. Thus the period required for the nymphal development of *G. musicus* tends to decrease at high temperatures and humidities.

Observations on the period for nymphal development in the field were made and it was concluded that it did not differ markedly from that under laboratory conditions. In the spring of 1945 the first hatchings occurred about September 19 and the first fliers had completed the final ecdysis by October 30. The majority of these swarms were on the wing at the end of the first week in November. The nymphal duration in the field during spring was thus between 41 and 48 days.

At Milman in 1946, eggs laid by the first generation fliers began to hatch on January 1. The first fliers were recorded from this locality on February 8, the period required in summer for the nymphal development of the second generation thus being about 39 days.

Some time must be passed by adult locusts after the final moult before egg-laying commences. This period is difficult to assess in the field, for it is practically impossible to follow the identity of one swarm. From very general field observations it is considered that at least 11 days are required for the maturation of the genital products. The incubation period for eggs in summer when ample moisture is available in the soil appears to be approximately 17 days. The autumn generation, from the time eggs hatch in summer until egg-beds are again established, requires a period of approximately 50 days. On the other hand, the spring generation, from the hatching of eggs to the establishment of egg-beds, occupies a period of approximately 55 days.

Table 11.

LIFE HISTORY DATA (IN DAYS) OF LABORATORY-REARED EXAMPLES OF *G. musicus*.

—	I.			II.			III.			IV.			V.			—
Series.	No.	Range.	Mean.	No.	Range.	Mean.	No.	Range.	Mean.	No.	Range.	Mean.	No.	Range.	Mean.	Mean Nymphal Duration.
1. In glass jars: crowded conditions (Oct.-Nov., 1945)	44	8–16	12·4	26	8–10	9	33	9–14	10·2	19	10–16	12·2	14	14–20	16·4	60·2
2. Ir. glass tubes: solitary conditions (Oct.–Nov., 1946)	12	6–12	9	6	7–9	8·5	4	8	8	3	8–11	9·7	1	15	15	50·2
3. In glass tubes: solitary conditions (Mar.–Apr., 1947)	27	6–10	6·3	25	4–10	6·1	18	4–10	7·6	11	8–12	10·1	3	14	14	44·1

Available information concerning the life-history stages recorded by various observers in central Queensland between 1939 and 1947 is tabulated (Table 12). Allowing for a considerable overlapping of generations during less favourable years, it may be concluded that there are normally two generations in this area.

On three occasions a partial hatching of eggs laid by the autumn generation of fliers has been recorded. This phenomenon was first observed at Kabra, where fliers established an egg-bed during the last week of February, 1944. These fliers had developed from eggs laid in the Westwood-Kalapa area by fliers of the spring generation which had migrated from the districts further west in December, 1943. The egg-bed at Kabra had therefore been established by fliers of the second generation. Hoppers emerged from this egg-bed during the latter half of March and formed bands which disappeared after light rain at the end of the month.

First-generation fliers invaded the Pioneer Valley, west of Mackay, in December, 1943 and January, 1944 and established egg-beds. Hopper bands appeared in January and the resultant fliers of this second generation reached their greatest density about mid-February. Numerous egg-beds were produced from which there was a partial hatching of nymphs during the first week of March. These hoppers apparently disappeared. The rest of the eggs remained dormant during the winter.

At Bouldercombe during February, 1947 egg-beds were established by fliers which had re-invaded this centre from districts further east. Apparently first-generation fliers had developed near Bajool and migrated north to the Fitzroy River flats. Here egg-beds were established and the second-generation fliers produced from these eggs invaded the Bouldercombe district. A minor hatching of eggs in these egg-beds occured in March, but no bands were formed and the individual nymphs either died or were dispersed.

The evidence appears to be conclusive that under certain conditions some of the eggs laid by second-generation fliers are able to hatch before the winter. In one instance only, such nymphs formed hopper bands, but these disappeared following light rains. It has not been ascertained whether the individual nymphs were merely dispersed by the rain or actually perished. The conditions responsible for the hatching of odd eggs, while the majority remains dormant until the following spring, are not known.

The occurrence of phase transiens does not make specific observations regarding its seasonal history possible. It is of interest to note that fliers which appear to belong to phase transiens were collected at Rockhampton during June and July, 1947, three months after the last flier swarms had died out. The biometrical data of this series were sufficiently different from that of similar fliers collected in the same locality during February and March to suggest that another generation had been completed. Apparently nymphal development is possible in phase transiens during March, April and May, though not in phase gregaria.

Table 12.

SEASONAL HISTORY OF *G. musicus*.

Compiled from available records—1939–47 outbreak in Central Queensland.

—	Eggs Hatched.	Nymphs.	Adults.	Eggs Laid.	Eggs Hatched.	Nymphs.	Adults.	Eggs Laid.
1939–40 ..	..	..	Nov., 1939	..	..	Feb. 1940	..	..
1940–41 ..	..	..	..	..	..	..	Jan. Feb. Mar. } 1941	..
1941-42 ..	..	Sept. Oct. Nov. } 1941	Oct. Nov. Dec. } 1941 Jan. 1942	..	..	Jan. Feb. Mar. } 1942	Mar. Apr. May } 1942	May 1942 ..
1942–43 ..	Sept. Oct. } 1942	Oct. Nov. } 1942	Nov. Dec. } 1942	..	..	Jan. Feb. } 1943	Feb. Mar. } 1943	..
..								
1943–44 ..	Oct. 1943	Sept. Oct. } 1943	Nov. Dec. } 1943	Jan. 1944	Jan. 1944	Dec. 1943 Jan. 1944	Feb. Mar. } 1944	Feb. Mar. } 1944
1944–45 ..	Aug. Sept. Nov. Dec. } 1944	Sept. Oct. Nov. Dec. } 1944	Jan. 1945	Feb. 1945	..	Mar. Apr. } 1945	..	..
1945–46 ..	Sept. Oct. } 1945	Sept. Oct. Nov. Dec. } 1945	Dec. 1945	Dec. 1945	Jan. 1946	Jan. 1946	Feb. Mar. } 1946	Mar. 1946
1946–47 ..	Sept. Oct. Nov. } 1946	Oct. Nov. Dec. } 1946	Dec. 1946 Jan. 1947	Jan. 1947	..	Mar. 1947	Feb. Mar. } 1947	Feb. Mar. } 1947

Data concerning the seasonal history of the solitary phase of *G. musicus* are lacking.

PARASITES AND PREDATORS.

Numerous natural enemies operate against the various life-history stages of *G. musicus*. Several parasites have been bred from eggs, nymphs and adults near Rockhampton and, in addition, a number of predators were recorded.

Egg Parasites and Predators.

Australia has a particularly rich Scelionid fauna, some 317 species being recorded by Tillyard (1926). To the genus *Scelio* belong a number of important locust egg-parasites. One of these, *S. bipartitus* Kieff., has frequently been bred from eggs of *G. musicus* and at times may be a useful factor in reducing an outbreak.

The method by which other Scelionids parasitize their hosts has been described (Uvarov, 1928) and it would seem feasible that *S. bipartitus* behaves in a similar manner. According to these descriptions, the parasites must oviposit in their hosts' eggs within 30 minutes of their being laid. Uvarov stated that it is only the moist accessory secretion of the locust egg-pods, and not the eggs themselves, which is attractive to the female parasites.

No observations were made on the actual process of parasitism of the eggs of *G. musicus* by *S. bipartitus*. At Mackay, Mungomery (1944) reported that this parasite began emerging from eggs in March and remained plentiful in the field until June. Near Rockhampton, it has been observed emerging from egg-pods at Alton Downs and Milman in April and May and at South Yaamba in late June. An odd parasite was still present in this last egg-bed area during the first week in August. In April, May and June, large numbers of the parasites were flying over the egg-bed within a few inches of the ground and also running rapidly over the soil surface as if in search of hosts. In the laboratory during June, the parasites were not induced to parasitize eggs laid in March which were taken from this and other egg-beds. They did, however, dig tunnels in the loose sand provided in the glass jar and in these they congregated. Without food in the laboratory they all died within 10 days.

If *G. musicus* is the sole host of *S. bipartitus*, the mechanism of parasitism and the seasonal history of this species are subjects of some importance. If freshly laid eggs only are parasitized, then the adults which emerge in late autumn and winter must survive until the spring generation of locusts establishes egg-beds—that is, usually in December.

An unusual predator of the eggs of *G. musicus* was discovered in several egg-beds at Alton Downs. This was *Dermestes ater* Degeer which, in common with other species of the family Dermestidae, normally feeds on dried animal remains. Larvae, pupae and adults were first noticed inside odd egg-pods in July, but it was thought at the time that this scavenger may have been feeding on the remains of non-viable eggs. The heavy clay-loam in which the egg-pods were located was extremely dry and as a result had fissured deeply. When the

egg-bed was again visited in September, it was apparent that *D. ater* had multiplied considerably and had apparently destroyed a large percentage of the egg-pods in this and another egg-bed on the same soil type near by. Larvae and adults were taken to the laboratory and fed readily on eggs of *G. musicus*. At the end of October it had destroyed most of the egg-pods in the two egg-beds in which it was first observed and odd larvae were discovered in other egg-beds established on lighter soil types. No further instance of this predator destroying locust eggs has been noted.

It is likely that the special conditions associated with the egg-beds attacked by *D. ater* can account for its unusual behaviour. Stockyards were located about midway between the two egg-beds on the heavy clay-loam and in such places its normal foodstuffs such as hides and particles of hair frequently abound. The deep fissures present in the soil at that time may have enabled the insect to gain access to the egg-pods in the first place. Apparently the abundance of such food enabled the beetle population to multiply enormously. It is probably significant that only odd larvae of *D. ater* were observed attacking egg-pods located in the lighter, non-fissuring soils in the same district.

Parasites and Predators of Nymphs.

One Tachinid parasite, *Tricolyga* sp. was bred from first and second instar nymphs collected at Gracemere in October. The hopper band was dense and numerous parasitic flies were flying actively amongst the nymphs and settling periodically on stones or other vantage points. A Tachinid egg, possibly of this species, was discovered on three of the first instar hoppers taken from a random sample. It was pale cream in colour and had been secured to the head of the host, just posterior to the eye.

At the same period an Asilid predator, *Bathypogon* sp., was very active in destroying first and second instar nymphs. The flies were quite numerous and attacked their prey in the manner typical of other members of the family. A fly would dart upon a nymph and, clutching it securely between its tarsi, would then retire to a convenient resting place to feed upon its victim.

Following the heavy monsoonal rains in central Queensland in February and March, 1947, a small green and brown frog, *Limnodynastes peronii*, became particularly common in Rockhampton and the surrounding district. At Rossmoya, hundreds of these frogs repeatedly attacked and finally destroyed a dense band of fifth instar nymphs of *G. musicus* feeding near a creek. When such insect food became insufficient to maintain the hordes of frogs, cannibalism soon reduced their numbers. Mungomery (1944) recorded the introduced toad, *Bufo marinus*, as feeding on nymphs of *G. musicus* when the bands reached the banks of a creek near Mackay.

At times birds have been reported feeding upon hoppers of *G. musicus*. The ibis, *Threskiornis spinicollis* Jameson, has been specially useful, but other species no doubt take their toll. On more than one occasion, crows, *Corvus cecilae* Mathews, were observed feeding on hoppers.

Parasites and Predators of Adults.

Flies of the sub-family Sarcophaginae are probably the commonest endoparasites of locusts and a number of species have been bred from fliers of *G. musicus* at Rockhampton. These include *Sarcophaga orchidea* Bott. and *S. eta* J.S.T. (the specific name in each case being open to doubt) and *Piocretia australis* J.S.T. Three other species have still to be determined.

In one case only did the parasites appear to be having any deleterious effect upon their hosts. This was at Alton Downs in April, where a small loose swarm was observed in which numerous individuals were hopping rather weakly over the ground, apparently unable to fly. A number of these fliers were collected and the three parasites named above were bred from them. Uvarov (1928) stated that the practical importance of larviporous flies in the control of locusts varies considerably with different species. The larvae of some species may be carried around by locust fliers apparently without in any way affecting their oviposition or other normal activities.

At times mites are common ectoparasites of fliers, though these were observed most frequently on isolated individuals. The mite nymphs favoured the veins of their hosts' yellow hindwings and when plentiful appeared to hamper the locusts' flight.

A Sphecid, *Chlorion saevus* Serv., was reported in 1940 from Charters Towers and Longreach exerting a remarkable control of flying swarms of *G. musicus*. Wasps of this family commonly prey upon locusts, but particular interest was centred in this report because it is quite unusual for wasp populations to reach a density sufficient to actually wipe out a locust swarm. The local increase could conceivably have been linked with a previous high locust population.

CONTROL.

In Queensland, the distribution of poisoned bran bait containing arsenic pentoxide as the toxic ingredient has been the method recommended for the control of locusts. However, with the advent of certain newer contact insecticides, it seemed desirable that their effectiveness against *G. musicus* should be ascertained. Various contact insecticides, including DDT and benzene hexachloride, and poisoned baits containing arsenic pentoxide, have figured in the preliminary trials described below.

Sprays and Dusts.

Stomach poisons may be applied to the foliage to be devoured by the hopper band and contact insecticides may be applied to the hoppers themselves or to the foliage and ground frequented by them. Both sprays and dusts may be used. Arsenicals applied in this way have been effective in the past as stomach poisons, but the danger of stock having access to poisoned fodder makes their use hazardous. Oils or oil emulsions, on the other hand, have shown promise as contact insecticides, yet the cost of these sprays is usually prohibitive.

Both power kerosene and dieselene were used by landholders near Rockhampton against small compact bands of first and second instar nymphs. Though these materials killed almost instantaneously all hoppers with which they came in contact, it was necessary to apply them at the rate of about 75 gallons per acre to effect complete control. The actual rate varied with the density of the vegetation. The cost of materials and application is well above that of the standard poisoned bait mixtures and therefore they cannot be recommended, except perhaps to destroy very small hopper concentrations when other materials are not at hand. All grass receiving this treatment is killed.

DDT dusts containing 2% para para isomer were tested against the early instars both in the laboratory and in the field. In the laboratory, first and second instar nymphs placed in jars lightly dusted with 2% DDT dust showed symptoms of partial inco-ordination of movement within one hour. At the end of three hours these symptoms were much more severe. Some of the nymphs were then lying on their sides with their legs moving spasmodically. All but a few had been completely overcome within five hours of treatment, while the remaining individuals were able to crawl only feebly. Complete mortality was obtained within 18 hours.

Field trials with 2% DDT dust were carried out against hopper bands at Gracemere in 1945. In the first test, a band of first instar nymphs approximately 0·37 acre in extent was dusted at the rate of 34 lb. per acre. An untreated band was used as a control. The dust was applied by means of a rotary hand duster between 9.45 and 10.45 a.m. At this time a light breeze was blowing which no doubt reduced the effective dust application. A narrow strip, about 10 feet in width, around the margin of the band was dusted first and then the remainder of the band was covered as systematically and as well as possible. Such a coverage was rendered difficult, for the movement of the duster operator stimulated hopper activity. There was a tendency therefore for the hoppers to keep surging beyond the original dusted margin and so avoid direct treatment.

Observations were carried out six hours later, for it was anticipated that the identity of the treated band would be lost if observations were delayed longer. Although considerable numbers of nymphs were seriously affected by the insecticide, the total percentage mortality was disappointing. Those which had escaped had formed a dense band beyond the treatment area. Any definite estimate of the percentage mortality would have been most unreliable, but it was considered that it did not exceed 30. It is likely that the poor result could be attributed partly to the unsuitable time of application, for the nymphs are particularly active at this time of the morning and their period of actual contact with the treated area must have been very short indeed.

A second trial was carried out near-by on the following day at 9.00 a.m., the dust being applied with the rotary duster at approximately 40 lb. per acre. In this case, however, a strip of only about 15 to 20 feet of the margin of the swarm was treated, beginning at the outside and gradually working inwards in a spiral formation. This method tended to prevent the hoppers commencing

any rapid migration from the treated area while the treatment was in progress. Observations carried out 8 hours later showed that the hoppers had migrated from the treated area and had formed a band not far away. A poor to fair kill had been obtained but it was not sufficiently high to prevent the aggregation of the unaffected hoppers into an appreciable band.

The third trial, also with 2% DDT dust, was commenced just before dusk against second instar hoppers which had camped for the night. Dense concentrations of the nymphs remain stationary for several hours during the night and furthermore dusting conditions were ideal after the breeze had dropped. An irregularly shaped area was treated at the rate of about 30 lb. of dust per acre, particular attention being paid to the densest masses of hoppers congregated on logs, fence-posts, &c. In this case, little or no dust was applied outside the margins of the band. Localized activity was stimulated while the dust was being applied but, unlike the bands treated earlier in the day, no mass movement of hoppers was evident. Observations carried out 15 hours later showed that a reasonably good kill had been effected, an estimate of about 70% mortality being made. It was not quite clear whether the remnants of this band actually aggregated again a day or two later, for other hopper bands were active in the vicinity.

Since DDT is a contact insecticide capable of maintaining a residual effect over a period, it was decided to test the value of DDT dusts applied to an egg-bed when hatching had commenced. An egg-bed at Bouldercombe was well suited to the trial, for here dense concentrations of egg-pods were restricted to a number of shallow depressions some five to 30 feet in diameter, interspersed by higher ground which apparently had been unattractive to the ovipositing female. Two of these depressions and a near-by small band of first instar nymphs were treated with a 2% dust, while two other depressions and another hopper band were treated with a 4% dust. Treatment was carried out at 6.30 a.m., before hatching had commenced for that day. Nine hours later the treated areas were examined and a comparison of the number of dead hoppers in each case made.

A reasonably high percentage mortality had resulted in the 4% DDT treated nymphal band and an estimate of 80% kill was made. The percentage mortality in the case of the 2% DDT treated band was lower, 50 to 60% being an approximate estimate. The hoppers had remained comparatively inactive in the treated areas for a sufficient time to allow the slow-acting insecticide to take effect.

Hoppers were still hatching from the egg-pods at the time of observation, but large numbers of dead and dying were present in three of the four treated depressions. Some dead hoppers were present in the fourth, but apparently only a few egg-pods had hatched. Unfortunately, no satisfactory basis for comparison of the two dusts could be devised. Heavy rain that night filled the depressions with water, thus preventing further observations.

From these preliminary data, it seems possible that DDT dusts may play a limited part in control practice. Since they are comparatively slow in their action upon nymphs of *G. musicus*, a long period of contact with the insecticide is required before a satisfactory kill is obtained. This condition is not fulfilled when bands are treated at the time of their maximum activity. Furthermore, windy conditions must reduce drastically the effective dust coverage.

Only one trial using benzene hexachloride dust against the nymphs of *G. musicus* was arranged. The dust contained 0·52% gamma isomer of BHC and was applied at the rate of approximately 30 lb. per acre to a band of fourth and fifth instar nymphs feeding on dense summer grass in a young citrus orchard at Barmoya. Treatment was carried out at 11.30 a.m. by means of a rotary hand duster. Again the dusting operations tended to stimulate the hoppers to mass movement away from the treated area. Moulting was in progress when the dust was applied. Observations were made 5½ hours later; though one or two small patches of hoppers appeared to have been little affected, about 50% were estimated to be already dead or dying. Many of the remainder showed minor symptoms of inco-ordination of movement and the final mortality was probably much higher than 50%, though it was not possible to make further observations.

A feature of the benzene hexachloride dust was the rapidity with which initial symptoms appeared in the treated hoppers. Before treatment was completed many individuals were already lying on their sides and kicking feebly. Others were obviously badly affected. The most important criticism of this treatment, and one which applies to any dust applied with hand dusters, is that the dusting operations tend to stimulate the hoppers to mass movement away from the dusted area. This might again be largely obviated if the insecticide was applied in the evening or in the early morning. It is also probable that by moulting many of the nymphs escaped the effects of the dust which had actually settled on them.

Poisoned Baits.

Since poison baiting is the method generally accepted in locust control work as the most economical in labour and materials, baiting trials were of primary importance. Three lines of research seemed necessary. First, to confirm the reported effectiveness of the recommended bran-arsenic pentoxide-molasses bait against *G. musicus*; second, to test alternative carriers for arsenical or other poisons; and third, to test benzene hexachloride as the toxic ingredient of bran baits.

Tests with Arsenical Baits.

The bran bait recommended for use against locusts in Queensland contains the following ingredients: ½ lb. arsenic pentoxide, 4 lb. molasses, 2½ gallons water and 24 lb. bran (Weddell, 1944). A number of graziers and farmers in the Rockhampton district used baits made up according to these directions in 1945, with variable results. In more than one instance the low percentage mortality which resulted was ascribed to the rapid desiccation of the bait

following distribution. The standard bait applied during the morning on a cloudless October day soon became quite dry and probably unpalatable. This effect was not so apparent when baits were distributed in cloudy weather. It was decided therefore to test baits containing either more molasses or more water. Weddell (1937) suggested that the molasses in bran baits makes them attractive to *Chortoicetes terminifera* over a longer period, particularly in dry weather.

Four third instar hopper bands, each about 1·25 acres in area, were chosen for the trial. Two bait mixtures were used and each was replicated twice. In one treatment the molasses of the standard bait was increased from 4 to 6 lb. and in the other the water was increased from 2½ to 3 gallons. The friability of neither of these mixtures appeared to be adversely affected by the increase in either molasses or water. The baits were broadcast by hand at the recommended rate of approximately 36 lb. dry bran per acre.

It was not found practicable to treat strictly comparable bands. Three were feeding on short green grass interspersed by areas of tussocky dry grass and bare ground. The fourth had partly invaded an area of rich green paspalum on a small flat. The baits with the extra molasses were distributed between 9.30 a.m. and 12 noon and those with extra water soon after noon. Rough estimates were made of the percentage mortality in each band 24 hours after treatment. In bands treated with the bait containing 6 lb. molasses to 24 lb. bran, approximately 70 to 80% mortality was estimated, while about 90% mortality and over was estimated in the bands treated with bait containing extra water. The kill in the fourth band was particularly spectacular, for the bran bait was apparently more attractive to the hoppers than the lush paspalum grass upon which they were feeding. Dead hoppers were strewn over the green grass and were congregated in masses in hollows and at the base of stumps and fence-posts.

Following this trial, a bran bait containing ½ lb. arsenic pentoxide, 6 lb. molasses, 3 gallons water and 24 lb. bran was used with spectacular results at Alton Downs against five bands of third and fourth instar nymphs. There appeared to be little tendency for the bait to aggregate into lumps during broadcasting, if ordinary care was exercised. When distributing the bait the rate of application was varied according to the density of the hoppers in the band. In each case the band was advancing as it fed on the native grass pasture and, as is usual under such conditions, dense concentrations of nymphs were found at the front of the moving band. The rate of application was increased where these dense masses occurred, whereas it was light over the remainder of the band and in the 18-foot marginal area beyond the limits of the band which was also treated. Twenty-four hours after treatment very few living hoppers could be found in the vicinity of any of the treated areas.

The result of these tests encouraged a group of farmers at Alton Downs to make a co-operative effort to destroy the numerous bands in their district. Twenty-eight bags of bran were used for the purpose and highly satisfactory

results were obtained. This appears to confirm the value of a bran-arsenic pentoxide-molasses bait in the control of *G. musicus*.

Benzene Hexachloride Baits.

Overseas reports suggest that BHC used in poisoned baits is more toxic to locusts than the arsenicals in general use. Furthermore, this material is relatively non-toxic to higher animals.

On two occasions, field trials with bran baits incorporating BHC as the toxic ingredient were carried out near Rockhampton. Both tests indicated that these baits are much more efficient against *G. musicus* than the standard arsenic pentoxide-bran bait.

In the first test, a bait containing 15 oz. of a 15% BHC mayonnaise emulsion, 4 lb. molasses, 2½ gallons water and 24 lb. bran was compared with the standard bait containing ½ lb. arsenic pentoxide, 4 lb. molasses, 2½ gallons water and 24 lb. bran. Thus, whereas the arsenic pentoxide content of the standard bait was 2% of the dry bran by weight, the gamma isomer content of the BHC bait was 0·073% of the dry bran by weight.

Four small bands of third instar nymphs were treated, each treatment being replicated twice. The baits were broadcast at 4.00 p.m. and the rate of distribution in the second benzene hexachloride treatment was less than the usual 36 lb. dry bran per acre.

Observations were made 24 hours after treatment. There was quite a spectacular kill in the first benzene hexachloride treatment, a mortality of some 90% being estimated. Dead hoppers were accumulated in depressions and at the base of clumps of grass and other vegetation. Many were still kicking feebly, while others were hopping around in a weak, inco-ordinated manner. These would almost certainly have died. In the second band treated with benzene hexachloride, the mortality appeared to be slightly lower, possibly because of the lighter treatment rate. Here again, however, the kill was regarded as quite satisfactory, an estimate of 70 to 80% mortality being made.

The kill was disappointing in both of the bands treated with the arsenical bait. An estimate of slightly less than 50% was made in each case. This may have been due partly to the fact that the bait was distributed too late in the day, when feeding was reduced in intensity. If this is correct, then it is possible that even better results would have been obtained with BHC had the treatments been carried out earlier in the day.

A second small test comparing BHC with arsenic pentoxide as the toxic ingredient in bran baits was conducted in conjunction with the trial of bagasse to be described later. In this non-replicated trial the arsenical bait contained ½ lb. arsenic pentoxide, 4 lb. molasses, 3 gallons water and 24 lb. bran, while the other contained 12 oz. of a 15% BHC mayonnaise emulsion, 4 lb. molasses, 3 gallons water and 24 lb. bran. The arsenic pentoxide content was therefore 2% and the gamma isomer content 0·061% respectively of the dry bran by weight.

These baits were broadcast in bands of second instar nymphs at 10.30 a.m. at the rate of approximately 36 lb. dry bran per acre. After 24 hours the percentage mortality in the arsenic pentoxide bait treatment was estimated as below 50%, whereas that in the BHC treatment was probably greater than 80%. In the latter, only a very small band of low concentration escaped. Even numerous fliers which had mingled with the dense hopper band had succumbed.

These admittedly inadequate tests of BHC would suggest that it will probably play a very important role in future campaigns against *G. musicus*.

Alternative Carriers for Baits.

During much of the 1939-47 outbreak in central Queensland, bran was not available in large quantities for use in poisoned baits. Accordingly, other materials were sought which might be substituted for at least part of the bran and yet not unduly reduce the effectiveness of the baits. Any alternative carrier needs to be readily available within a reasonable distance of the infested area, at a cost in proportion to its effectiveness. Ground peanut shells and bagasse (a sugar-cane by-product) were used in preliminary tests, but neither showed particular promise. By increasing the water content of such baits more satisfactory results may have been obtained.

Ground Peanut Shells.—Two small second instar bands of about 0·25 acre each were treated with a bait consisting of ½ lb. arsenic pentoxide, 4 lb. molasses, 2½ gallons water and 24 lb. ground peanut shells. The peanut-shell meal was prepared by grinding the shells to about the consistency of wheat bran in a hammer mill. The bait was broadcast about 10.00 a.m. at the rate of approximately 36 lb. dry material per acre.

Observations on the effectiveness of the bait were made 24 hours later, but the percentage kill proved to be disappointing. The majority of the hoppers in each band was unaffected by the bait. The bait appeared to have dried out much more rapidly than is the case with the standard bran bait. A larger quantity of water may have increased its palatability, though the material appeared to be capable of absorbing much less water than bran.

Bagasse.—This material has been used successfully in poisoned baits in East Africa against *Schistocerca gregaria* Forsk. (Notley, 1946). Hoppers of this species fed readily on bagasse baits, though in attractiveness tests on adults and nymphs wheat bran was significantly more attractive than bagasse.

A sample of bagasse was supplied by the Moreton Sugar Mill, Nambour, for trials against *G. musicus* in 1946. The particulate size of typical samples of this material is shown in Table 13.

Bagasse is capable of absorbing a much greater volume of water than is an equal weight of bran. It was assumed, when mixing the baits, that volume for volume bagasse and bran could be distributed over an equal area of grass-hoppers and therefore ½ lb. arsenic pentoxide would be sufficient either for 24 lb.

Table 13.

PARTICULATE SIZE OF BAGASSE.

Seive.	Percentage Retained.	
	Sample A.	Sample B.
mm.		
18	11·2	12·2
18–10	25·4	23·6
10–5·5	20·6	16·1
5·5–3·5	12·1	12·2
3·5–1·6	10·4	17·1
1·6–0·6	13·5	12·9
0·6	0·6	6·0

bran or an equal volume of bagasse, namely 8 lb. The following were the ingredients of the baits used:—

(i.) Arsenic pentoxide ½ lb., molasses 4 lb., water 3 gallons and bran 24 lb.

(ii.) Arsenic pentoxide ½ lb., molasses 4 lb., water 3 gallons and bagasse 8 lb.

Thus, whereas the bran bait was broadcast at the rate of approximately 36 lb. dry bran per acre, the bagasse was broadcast at the rate of 12 lb. dry bagasse per acre.

The baits were distributed over two almost adjacent bands of second instar nymphs between 10.30 and 11.00 a.m. One band was located on ground bearing a very short green grass shoot following burning, while the other was on unburnt country bearing dry, tussocky grass about 6 to 12 inches high, amongst which there was a noticeable short green shoot. Being lighter than the bran bait, the bagasse was somewhat more difficult to broadcast evenly, especially in a moderate breeze, though there were no other factors adversely affecting distribution.

Observations made 24 hours after treatment were difficult, for the hoppers which had escaped from each treated area had merged into one band. However, judging by the numbers of dead hoppers in and immediately around the baited areas, there was little difference in the effectiveness of the arsenic pentoxide-bagasse bait and the arsenic pentoxide-bran bait. The percentage mortality in either case would not have exceeded 50%.

Attractiveness of Baits.

The use of attractants in locust baits dates back at least to 1892 (Morrill, 1919), when molasses was added to a cutworm Paris green-bran bait for the control of grasshoppers. It was believed that the addition of molasses would assist the particles to adhere to one another and to render the bait attractive to

the pest for a longer period. However, the actual value of the molasses content of baits has been questioned by a number of workers and, in fact, many locust campaigns have been conducted in which molasses has been omitted from the arsenical baits.

More recently attempts have been made to devise a suitable experimental technique to compare the attractiveness of baits containing various materials. The most successful method of comparison is generally known as the pan-bait method. The baits to be tested are spread in small quantities on pans or trays and the grasshoppers feeding at each bait are counted at intervals during the day. The whole series of baits is replicated a number of times and the position of the baits in each series is randomized. It is assumed that the bait which has the largest number of grasshoppers feeding at it is the most attractive (Morrill, 1918; Ford and Larrimer, 1921; Painter *et al.*, 1925).

Shotwell (1942) carried out further series of pan-bait experiments and also reviewed the earlier work. He concluded that attractants such as molasses, amyl acetate, lemons and salt do not increase the attractiveness of bran baits to grasshoppers.

Allman (1946) suggested the possibility of BHC being actually attractive to grasshoppers. If this was correct, then molasses could serve no useful purpose in BHC-bran baits and would increase their cost unnecessarily.

Baits incorporating a mixture of low-grade flour and sawdust (1:13 by volume) instead of bran have been used successfully against grasshoppers in Canada since 1938 (Paul and King, 1944). Equal volumes of sawdust and bran are recommended by McCarthy (1946) as the carrier in baits against *Chortoicetes terminifera*.

A pan-bait experiment designed to compare the attractiveness of arsenic pentoxide and BHC-bran baits, with and without molasses, was conducted against second instar nymphs of *G. musicus* near Rockhampton. The opportunity was also taken to compare the attractiveness of bran baits with those incorporating mixtures of flour and sawdust and bran and sawdust as the carrier.

The following 10 baits were used in the experiment, the ingredients being measured accurately in reduced quantity in the laboratory the day before the test. The baits were mixed on the morning of the experiment and transported separately in screw-top jars to prevent any desiccation before exposure. The percentages of arsenic pentoxide and the gamma isomer of BHC of the dry carrier by weight are included in parenthesis:—

1. Arsenic pentoxide ½ lb., molasses 4 lb., water 2½ gallons, bran 24 lb. (= 2% arsenic pentoxide).
2. Arsenic pentoxide ½ lb., water 2½ gallons, bran 24 lb. (= 2% arsenic pentoxide).
3. BHC 10% dust 1 lb., molasses 4 lb., water 2½ gallons, bran 24 lb. (= 0·052% gamma isomer).
4. BHC 10% dust 1 lb., water 2½ gallons, bran 24 lb. (= 0·052% gamma isomer).
5. BHC 15% mayonnaise emulsion 10 oz., molasses 4 lb., water 2½ gallons, bran 24 lb. (= 0·049% gamma isomer).

6. BHC 15% mayonnaise emulsion 10 oz., water 2½ gallons, bran 24 lb. (= 0·049% gamma isomer).
7. Arsenic pentoxide ½ lb., water 2½ gallons, sawdust and bran (50: 50 by volume) 24 lb. (= 2% arsenic pentoxide).
8. BHC 10% dust 1 lb., water 2½ gallons, sawdust and bran (50: 50 by volume) 24 lb. (= 0·052% gamma isomer).
9. Arsenic pentoxide ½ lb., water 2½ gallons, sawdust and flour (85 : 15 by weight) 24 lb. (= 2% arsenic pentoxide).
10. BHC. 10% dust 1 lb., water 2½ gallons, sawdust and flour (85 : 15 by weight) 24 lb. (= 0·052% gamma isomer).

Thirty grey cardboard trays measuring 12 inches by 7½ inches with ½ inch vertical sides were used for the experiment. These were divided into three groups of 10 and numbered consecutively in each group. Small quantities of each bait were spread in a thin layer over the bottom of each tray having the corresponding number. The 10 treatments were then arranged in three groups within a large band of hoppers. The position of each bait was randomized within each replication. Their positions were again randomized when the baits were renewed once during the progress of the experiment. It was believed that the baits containing sawdust dried out much more rapidly than the bran baits and might prove unattractive for that reason alone.

The first count of hoppers which were apparently feeding on each tray was made at 10.20 a.m. Four further counts were made at intervals until 12.30 p.m. When the experiment began, the temperature at the surface of the ground with the bulb of the thermometer covered lightly with fragments of grass was 118° F. The sun was shining, though the sky was partly overcast. Heavy black clouds had obscured the sun by 12.30 p.m., when the temperature at the ground surface had dropped to 89° F. Thereafter the number of hoppers feeding was reduced to a very low level and it was decided to discontinue counts. The hoppers tended to crowd together on various objects, reminiscent of their behaviour toward nightfall. Heavy rain began to fall at 3.0 p.m.

Analysis of the data has been carried out using the transformed variable $\sqrt{x + \frac{1}{2}}$. All the treatments have been included in the analysis of variance to determine the relative attractiveness of the various carriers. However, since molasses was incorporated only in the baits using bran as a carrier, treatments 1 to 6 have been analysed to determine the value of molasses as an attractant.

The difference between the number of nymphs attracted to the bran baits and the baits containing sawdust and bran or sawdust and flour is highly significant (Table 14). The difference is so marked that it would suggest that neither of the alternative carriers should be considered for general use when bran is available.

The F value for the analysis of treatments 1 to 6 is significant at the 5% level. The baits containing molasses (Nos. 1, 3 and 5), as well as the arsenic pentoxide-bran bait without molasses (No. 2) are significantly more attractve than the BHC baits without molasses. There is no significant difference, however, between arsenic pentoxide-bran baits with or without molasses.

Table 14.

RELATIVE ATTRACTIVENESS OF BAIT CARRIERS TO *G. musicus*.

Bait Ingredients.	Mean.	Equivalent Mean Value (original units).
1. Bran, arsenic pentoxide, molasses	6·58	42·75
3. Bran, BHC dust, molasses	6·48	41·53
5. Bran, BHC emulsion, molasses	6·39	40·29
2. Bran, arsenic pentoxide	6·15	37·28
4. Bran, BHC dust	4·77	22·22
6. Bran, BHC emulsion	4·57	20·42
9. Sawdust 85%, flour 15%, arsenic pentoxide	3·06	8·86
7. Sawdust 50%, bran 50%, arsenic pentoxide	2·91	7·99
8. Sawdust 50%, bran 50%, BHC dust	2·20	4·35
10. Sawdust 85%, flour 15%, BHC dust	1·76	2·60
Necessary difference for significance :		
Analysis all 10 treatments—5%	1·13	
1%	1·55	
Analysis treatments 1 to 6—5%	1·27	
1%	1·81	

It may be concluded, therefore, that molasses as an ingredient of the standard arsenic pentoxide-bran baits does not increase their attractiveness while fresh to nymphs of *G. musicus*. Nevertheless, it is possible that even in these baits the addition of molasses may be advantageous if it enables the bait to maintain its attractiveness over a longer period. It appears that molasses does decidedly increase the attractiveness of baits incorporating BHC as the toxic ingredient and that BHC is not in itself attractive to *G. musicus* nymphs. If BHC, therefore, is to be substituted for an arsenical in the recommended bran baits against this species, it will be desirable to include molasses in the bait formula.

Variability of Baiting Results.

At times unsatisfactory results are obtained with poisoned bran baits against *G. musicus*, even when the directions for mixing and distributing the bait are followed carefully. The efficiency of baiting operations no doubt is determined by a number of inter-related factors, some of which appear to be noteworthy.

An understanding of the behaviour of the nymphs of this species in relation to temperature, wind and cloud would certainly improve the somewhat haphazard nature of control operations. Before any bait will give satisfactory results, it must be made available to the hoppers when they are feeding most actively. The intensity of feeding at any given hour of the day is governed largely by temperature and sunlight and perhaps even by wind velocity. Thus at each period of the year there is an optimal time of day for bait distribution. This naturally varies with day-to-day fluctuations in weather. From general observations, the optimal time for bait distribution for the spring generation is

before 11.00 a.m. and for the summer-autumn generation before 10.00 a.m. When temperatures are highest, it is likely that a second burst of feeding activity occurs in the afternoon when the heat of the day has passed.

Heavy cloud undoubtedly reduces feeding, though light cloud does not appear to interfere noticeably when temperatures are high.

One rather important practical aspect of successful control by the use of poisoned baits deserves mention. As already stated, nymphs cease to feed for some hours prior to and do not recommence feeding for some hours following each ecdysis. Though no exact data have been collected as to the actual period during which the nymph fasts at each moult, observations in the laboratory suggest that these facts account for an important portion of the larval life. Seldom do all nymphs in a larval band moult on the same day. Though in many instances this process may be spread over several days, especially when hatching has been prolonged from any one egg-bed, in some cases moulting for the band would be completed in about two or three days. The curve of the actual percentage of moulting nymphs in a given band plotted against time would in all probability closely resemble the normal curve. If the nymphal duration is regarded as approximately 45 days, a 100% mortality is theoretically not possible during some 10 to 15 days of this period (that is, if each of the five ecdyses requires two to three days for completion). As the time of bait application tends to coincide with the maximum percentage of nymphal ecdysis, so the theoretical possible mortality decreases. Even with a perfect bait applied to the most homogeneous band—that is, one composed of nymphs which all hatched on the same day—the probability of a 100% mortality is only about 80%.

In one instance at least, it was ascertained that a very minor mortality followed baiting with the arsenic pentoxide bait when it was distributed at a time coinciding with ecdysis in the majority of hoppers. Two hours after baiting this band of fourth instar nymphs, samples were collected by sweeping and placed in jars in the laboratory for further observation. By the following day the majority of the nymphs had moulted to the fifth instar and only odd individuals had died. Similar results were observed in the field.

Economic Status of *G. musicus* and the Practicability of Control.

As has been pointed out, the normal food-plants of *G. musicus* are confined almost entirely to the Gramineae. This family includes the native grasses and a number of introduced pasture grasses and crop plants. Attacks upon crops belonging to other botanical families appear to be accidental.

This food preference has an important bearing upon the economic importance of the species. Outbreak areas in central Queensland are confined to pastoral districts, but in the infestation area sugar-cane and other valuable crops may be threatened by invading swarms. Frequently, maize, sorghum and Sudan grass are destroyed. The effect of an attack upon sugar-cane apparently depends largely on the associated weather conditions. Severe damage has been caused

when an attack has coincided with poor growing conditions, though recovery was possible when rain followed (Mungomery, 1944). Generally, the effect of cane defoliation appears to be indirect, for weed growth follows the opening up of the foliage canopy.

Uvarov (1944) emphasized the importance of the outbreak areas in locust infestations, for once these are known it may be possible to keep them under observation so that incipient swarms can be dealt with by recognized control methods. Such a preventive policy may be practicable ultimately, though a much more exact ecological study of *G. musicus* is necessary before future outbreaks can be forecast and dealt with in this way.

As swarms extend beyond the outbreak area, effective control becomes much more difficult. Much of the infestation area in central Queensland is occupied by large pastoral holdings where the plotting of egg-beds and the subsequent destruction of hopper bands appear to be far from practicable. Large swarms of fliers are thus able to develop and invade the more limited agricultural areas. The control of hopper bands which might menace standing crops in the more closely settled areas is strongly recommended, but frequently this action merely postpones the attack by invading flier swarms from farther afield. In many cases, however, a temporary postponement of an attack for even three or four weeks, particularly when feed is scarce, may be very valuable to the farmer. Co-operation by groups of farmers when instituting control measures under such circumstances is of the utmost importance.

The actual method of control to be used to combat *G. musicus*, whether in incipient swarms in the outbreak areas or in denser swarms threatening agricultural crops, will almost certainly be by means of poisoned baits. Aerial distribution of contact insecticides or baits would appear to be completely impracticable against this species owing to the relatively small and scattered nature of the hopper bands to be treated.

Though arsenic pentoxide is quite effective in baits, it is likely that BHC will supersede it as the toxic ingredient. The use of a poison which is relatively non-toxic to higher animals is very desirable from the psychological point of view, for then only can the full co-operation of landholders be expected.

CONCLUSIONS.

An extensive outbreak of the yellow-winged locust, *Gastrimargus musicus* Fabr., occurred in central Queensland between 1939 and 1947. The source of this outbreak has been traced to an area embracing Logan Downs-Clermont-Peak Downs, though other minor outbreak areas possibly contributed. The progress of the migrations of swarms from this area has been followed and the approximate limits of the infestation area in central Queensland plotted. This area includes a large tract of country from beyond Clermont and Emerald in the west, Springwood, Moura and Mt. Larcom in the south and Yacamunda and Proserpine in the north. The coastline from Proserpine to Mt. Larcom forms the approximate eastern boundary.

Gregarious and solitary phases of the species have been distinguished. Phase solitaria is very variable in colour with green and dark-brown males and green females predominating. Medium-brown males and dark-brown females predominate in phase gregaria. The pronotum is relatively longer, narrower, and more convex and the E/F ratio is lower in phase solitaria. The degree of sexual dimorphism is also greater in samples from an isolated population.

Egg-beds are usually located on relatively bare ground, the concentration of egg-pods varying in any given egg-bed according to the suitability of the soil at oviposition. Cultivated land is sometimes utilized. The number of eggs per egg-pod averaged 39, but apparently shows a marked variation.

The chorion of the egg bears a characteristic hexagonal pattern of small protuberances and near the posterior pole there is a ring of 46 to 48 funnel-shaped micropylar canals which allow the entry of the spermatozoa. The embryos of overwintering eggs in all cases were in the pre-blastokinesis stage of development. Embryonic development proceeds only when moisture is available and the temperature exceeds a certain minimum. In the absence of moisture, eggs have remained viable for at least 10 months. Development in the embryo is associated with an increase in the dimensions and weight of the egg. Immersion of eggs in water for periods of up to seven days retarded, but otherwise did not interfere greatly with, normal hatching.

Aggregations of hopper bands usually occur in the vicinity of the egg-bed, though sometimes band formation does not follow substantial hatchings. The dense masses of nymphs behave as a single unit, the movement of one individual stimulating a similar movement in its neighbours. Their wanderings appear to be usually without regard to direction and may result in the merging of a number of smaller units. Feeding is most marked during the morning, the time of day when feeding commences being influenced chiefly by temperature.

Major migrations of fliers usually occur in the autumn and are not undertaken because of food scarcity in their breeding grounds or in search of suitable oviposition sites. Prior to egg-laying, the swarm terminates its migration and indulges only in a short circling type of flight to and from its feeding grounds. Each night the fliers drift back to one restricted area which is used both for camping and subsequently as the egg-bed site. Mating occurs on the actual egg-bed and frequently each female is attended by one or more males while egg-laying proceeds.

In the laboratory, nymphs of the spring generation required 50·2 to 60·2 days for their development, whereas the summer-autumn generation required 44·1 days. This corresponds approximately to the time required for nymphal development in the field.

Normally, there appear to be two generations of the gregarious phase annually. Occasionally, however, eggs of the second generation hatch in autumn, though in no case have the hoppers reached maturity in bands. The disappearance of these nymphs may have been due to either mortality or dispersal. The

latter appears to be the more likely solution, for adults presumably belonging to phase transiens have been taken during July in Rockhampton. From the practical point of view, therefore, only two generations of phase gregaria are important.

Parasites and predators of all the life-history stages have been recorded at Rockhampton. Some, such as *Scelio bipartitus*, appear to be specific enemies of this locust, but others such as *Dermestes ater* may be accidental. In the coastal portion of the infestation area, parasites and predators seem to exert a very limited control.

Various control measures were tested and of these poisoned bran baits were the most effective. During spring in central Queensland, where high solar temperatures are associated with low humidity, the efficiency of the standard arsenic pentoxide-bran bait appeared to be improved when the water content was increased from 2½ to 3 gallons for every 24 lb. dry bran. Bran baits containing 0·06% of the gamma isomer of BHC seem to be even more effective than the arsenic pentoxide-bran baits.

In a test designed to indicate the relative attractiveness of various baits to second instar nymphs, molasses appeared to be a desirable ingredient of BHC baits. On the other hand, the addition of molasses to the arsenic pentoxide-bran bait did not increase its attractiveness. Baits incorporating mixtures of bran and sawdust and flour and sawdust as the carrier did not compare favourably with bran baits.

The success of baiting operations is affected not only by climatic factors such as temperature and light, but also by the relative abundance of moulting nymphs in the band at treatment. Nymphs cease to feed for some hours at each ecdysis and, if the distribution of baits coincides with the time of maximum moulting, unsatisfactory results may be obtained.

The food plants of *G. musicus* are confined almost entirely to the family Gramineae. Attacks on other crops appear to be accidental. The majority of the losses incurred by this species are, therefore, due to pasture damage, though severe localized losses may follow attacks on sugar-cane, maize, and sorghum.

Outbreak areas need to be carefully mapped so that ultimately control may be preventive in nature. Complete control once migrations from the outbreak areas have commenced appears to be impracticable. Temporary control by the use of poisoned baits is recommended to co-operative groups in order to reduce losses in agricultural areas.

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APPENDIX A.

SUMMARY OF REPORTS AND OBSERVATIONS OF SWARMS OF *G. MUSICUS* IN CENTRAL QUEENSLAND, 1939 TO 1947.

March-November, 1939.—Hopper bands and flier swarms reported from Glenden, west of Nebo.

November, 1939.—Eggs hatched at Glenden but hoppers died out. Flier swarms first reported near Clermont.

January, 1940.—Further hatchings of eggs at Glenden.

February, 1940.—Hopper bands noted on Logan Downs, north of Clermont. Flier swarms west of Nebo.

January, 1941.—Numerous flier swarms north-east of Capella.

February, 1941.—Flier swarms numerous within a radius of 15 miles of Capella; also east of Clermont.

March, 1941.—Fliers still present near Capella and Clermont though less numerous.

September-October, 1941.—Hopper bands on Logan Downs.

November, 1941.—Hopper bands extensive on Peak Downs, south-east of Clermont.

October-November, 1941.—Loose swarms of fliers on Logan Downs.

January, 1942.—Fliers up to 40 miles north of Clermont; one swarm flew south through Emerald at the end of the month.

January-February, 1942.—Hopper bands very dense on Logan Downs, at Clermont and between Clermont and Capella.

March, 1942.—Very dense and extensive flier swarms north, north-east and east of Clermont.

April, 1942.—Swarms spread farther north and east of Clermont; also south from Capella. Loose flier swarm three miles through reported between Clermont and Logan Downs and another four miles through between Clermont and Capella. Swarms observed at Emerald.

May, 1942.—Egg-beds established at Frankfield station, about 56 miles north-west of Clermont, on Peak Downs and on the Capella racecourse. Many other egg-beds probably established.

September, 1942.—Hoppers hatch from egg-beds, particularly east-north-east of Clermont, near the Isaacs River. Also some hatching at Capella. Feed scarce.

October-November, 1942.—Hatching of egg-beds over a wide area from Yacamunda in the north to Capella in the south, east to the Isaacs River and west to a point some 10 miles south-west of Clermont. Fliers again invade Emerald district from the north.

December, 1942.—Flying swarms over most of the area where hoppers were reported in November. Swarms have been observed further west.

January, 1943.—Large hopper bands reported for a distance of 40 miles north and north-east of Clermont, north of Capella and in the Emerald district.

February, 1943.—Flier swarms reported from the greater part of the Mackenzie River country, north of Dingo and east to Marlborough. The infestation to the north of Clermont considerably diminished. Flier swarms reported from Fernlees and Springsure; egg-beds established at Springsure.

March, 1943.—Flier swarms less numerous near Clermont; egg-beds probably established. Swarms reported moving in a northerly direction over an area of about 12,000 acres on northern side of the central western railway at Gogango.

September, 1943.—Hopper bands reported south of Nebo.

October, 1943.—Hoppers hatch from egg-beds in Clermont district.

November, 1943.—Flying swarms at Clermont. Swarms throughout Nebo district and have penetrated Pioneer Valley west of Mackay.

December, 1943.—Flier swarms extended to Grantleigh, Westwood and Kalapa, and Wowan and Dululu in the Callide Valley. Flying swarms active in Pleystowe, Finch Hatton and Eton Mill areas near Mackay. Hopper bands west and south-west of Clermont.

January, 1944.—Hopper bands very common in Clermont district, at Withersfield, Gogango, Grantleigh, Wowan, Dululu, Moura and in the Mackay district.

February, 1944.—Flier swarms in Mackay district; also at Kabra, Malchi and Gracemere, near Rockhampton.

March, 1944.—Flier swarms common from 40 to 70 miles north of Clermont; very few elsewhere in Clermont district; egg-beds established in Mackay district, at Kabra, Malchi and Gracemere; flier swarms at Ridgelands, north-east of Rockhampton.

August, 1944.—Egg-bed at Malchi hatches; hopper bands in Mackay district.

September, 1944.—Hopper bands at Gogango, Westwood, Bushley, Stanwell, Gracemere, The Caves, St. Lawrence and Marlborough. Some hopper bands die out because of food shortage in Mackay district.

October, 1944.—Swarms (probably hopper bands) reported from Nebo district. Hopper bands in Mackay district.

November, 1944.—Hopper bands fail to reach maturity at Kalapa and Mt. Morgan, apparently because of scarcity of food.

December, 1944.—Hopper bands in Mackay district, at St. Lawrence, Dululu and Kalapa. Some hopper bands die out at Rockhampton, Kalapa and The Caves.

January, 1945.—Flier swarms south and south-east of Clermont, especially between Capella and Emerald; also at Rockhampton.

February, 1945.—Flier swarms and hopper bands in Clermont district; also at Rockhampton, Gracemere, Mt. Morgan-Dululu, Marlborough; fliers migrate north of Pioneer River, in Mackay district, towards Proserpine. Here swarms smaller and looser than in 1944.

April, 1945.—Band of hoppers in last nymphal stage at Gracemere.

September, 1945.—Hopper bands at Gracemere, Westwood, Kabra, Malchi, Bouldercombe and Alton Downs.

October, 1945.—Further hatchings from egg-beds at Bouldercombe and Gracemere.

December, 1945.—Flier swarms at Gracemere; fifth instar hopper bands at Dululu; flier swarms begin establishing egg-beds at Alton Downs and at Milman and The Caves.

January, 1946.—Hopper bands at Milman and The Caves.

February, 1946.—Flier swarms at Milman.

March, 1946.—Egg-beds established at Parkhurst, Milman and Alton Downs.

August, 1946.—Large egg-beds at Clermont, Capella and Springsure.

September, 1946.—Hoppers hatch from egg-bed established at Bajool.

October, 1946.—Hopper bands at Barmoya, Etna Creek, Bajool, Greenlake. Some bands die out because of food shortage. Hoppers hatch from egg-beds at Alton Downs at end of month.

November, 1946.—Many hopper bands die out or disperse at Alton Downs; further hatchings also. Eggs hatch at Springwood, south-east of Springsure. Hatchings at Clermont and Capella and large bands of hoppers present.

December, 1946.—First instar hoppers attacking newly germinated Sudan grass at Milman; second instar hopper bands at Milman and Greenlake.

January, 1947.—Large loose and dense flier swarms at Glen Geddes and egg-beds being established. Flier swarms penetrate to coast at Yeppoon and Torilla where egg-beds have been established.

February, 1947.—Egg-beds hatch at Glen Geddes at beginning of the month. Flier swarms still active at Yeppoon; egg-laying in progress. Flier swarms return to Bouldercombe area from east and egg-beds established.

March, 1947.—Odd small dense swarms of fliers at Gracemere and large flier swarm ovipositing at Bouldercombe. Some eggs hatch in this egg-bed. Hopper bands at Rossmoya and Barmoya (fifth instar during third week). Flier swarms reported from Clermont. Loose and dense flier swarms at Barmoya; egg-beds established at South Yaamba.

September, 1947.—Eggs commence to hatch in egg-beds at Bouldercombe, The Caves, South Yaamba, Gracemere, St. Lawrence, Clermont and Springwood.

October, 1947.—Hoppers in second and third instar during first week near St. Lawrence. Bands containing all nymphal stages at Gracemere at end of month. Also bands near Bajool, Ambrose, Mt. Larcom and Clermont.

December, 1947.—Reports of hopper bands dying out at St. Lawrence, South Yaamba and Mt. Larcom. Odd small hopper bands at St. Lawrence. Flier swarms present near Clermont, but smaller than previously.

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